B 3 741 781

A TREATISE ON ZOOLOGY

EDITED BY

E. RAY LANKESTER

III

SHOUT
SHARE
IT

LIBRARY
UNIVERSITY OF
CALIFORNIA
SANTA CRUZ

QL
45
L28
1900a
V.3

Digitized by the Internet Archive
in 2007 with funding from
Microsoft Corporation

http://www.archive.org/details/treatiseonzoolog03lankrich

A TREATISE ON ZOOLOGY

A

TREATISE ON ZOOLOGY

EDITED BY

E. RAY LANKESTER

M.A., LL.D., F.R.S.

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE
OF FRANCE; DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS
OF THE BRITISH MUSEUM

PART III

THE ECHINODERMA

BY

F. A. BATHER, M.A.

ASSISTANT IN THE GEOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM

ASSISTED BY

J. W. GREGORY, D.Sc.

LATE ASSISTANT IN THE GEOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM
PROFESSOR OF GEOLOGY IN THE UNIVERSITY OF MELBOURNE

AND

E. S. GOODRICH, M.A.

ALDRICHIAN DEMONSTRATOR OF ANATOMY IN THE UNIVERSITY OF OXFORD

Reprint A.ASHER & CO. Amsterdam 1964

A
TREATISE ON ZOOLOGY

EDITED BY

dwin

E. RAY LANKESTER

M.A., LL.D., F.R.S.

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE
OF FRANCE; DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS
OF THE BRITISH MUSEUM

PART III

THE ECHINODERMA

BY

F. A. BATHER, M.A.

ASSISTANT IN THE GEOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM

ASSISTED BY

J. W. GREGORY. D.Sc.

LATE ASSISTANT IN THE GEOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM
PROFESSOR OF GEOLOGY IN THE UNIVERSITY OF MELBOURNE

AND

E. S. GOODRICH, M.A.

ALDRICHIAN DEMONSTRATOR OF ANATOMY IN THE UNIVERSITY OF OXFORD

LONDON
ADAM & CHARLES BLACK
1900

Exclusive Agents for U.S.A.
STECHERT-HAFNER SERVICE AGENCY, INC.
31 East 10th Street
New York, New York 10003

Sole agents for India:
Today & Tomorrow's Book Agency,
22-B/5, Original Road, Karol Bagh,
New Delhi-5

PREFACE

The present volume is the "Third Part" in order of a comprehensive treatise on Zoology, which has been for some time in preparation under my editorship. In this treatise each of the larger groups of the Animal Kingdom is to be described by a separate author; whilst, as far as possible, uniformity in method and scope of treatment is aimed at. The authors are, for the most part, graduates of the University of Oxford, though it may not be possible to maintain this limitation in future sections of the work.

The general aim of the treatise is to give a systematic exposition of the characters of the classes and orders of the Animal Kingdom, with a citation in due place of the families and chief genera included in the groups discussed. The work is addressed to the serious student of Zoology. To a large extent the illustrations are original. A main purpose of the Editor has been that the work shall be an independent and trustworthy presentation, by means of the systematic survey, or taxonomic method, of the main facts and conclusions of Zoology, or, to speak more precisely, of Animal Morphography.

The treatise will be completed in ten parts of the size of the present one. It will at once be apparent that this limitation necessitates brevity in treatment which, however, will not, it is believed, be found inconsistent with the fulfilment of the scope proposed or with the utility of the work to students. The immediate publication of the following parts may be expected:—

Part I. Introduction and the Protozoa.

Part II. General Discussion of the Metazoa—The Porifera — The Hydromedusae — The Scyphomedusae—The Anthozoa—The Ctenophora.

Part III. The Echinoderma (the present volume).

Part IV. The Mesozoa—The Platyhelmia—The Nemertini.

These parts will be issued, without reference to logical sequence, as soon as they are ready for the press. In accordance with this procedure, which to some extent evades the injustice of making an author, whose work is finished, wait for publication until other more tardy writers have completed their tasks, the present volume, which is Part III., is the first to make its appearance.

The following authors have undertaken portions of the work:— Professor Poulton, F.R.S., M.A. Oxon.; Professor Weldon, F.R.S., M.A. Oxon.; Professor Benham, D.Sc., M.A. Oxon.; Mr. G. C. Bourne, M.A. Oxon.; Mr. G. H. Fowler, M.A. Oxon.; Professor Minchin, M.A. Oxon.; Mr. F. A. Bather, M.A. Oxon.; Professor J. W. Gregory, D.Sc.; and Mr. E. S. Goodrich, M.A. Oxon.

E. RAY LANKESTER.

February 1900.

CONTENTS

CHAPTER VIII

General Description of the Echinoderma . . 1

CHAPTER IX

The Pelmatozoa—Cystidea 38

CHAPTER X

The Pelmatozoa—Blastoidea 78

CHAPTER XI

The Pelmatozoa—Crinoidea 94

CHAPTER XII

The Pelmatozoa—Edrioasteroidea 205

CHAPTER XIII

The Eleutherozoa—Holothurioidea . . . 217

CHAPTER XIV

The Eleutherozoa—Stelleroidea 237

CHAPTER XV

The Eleutherozoa—Echinoidea 282

INDEX 333

TABULAR STATEMENT SHOWING THE SYSTEMATIC POSITION OF THE ECHINODERMA.

ANIMALIA.

GRADE I. PROTOZOA.
" II. METAZOA.

BRANCH A.	BRANCH B.
PARAZOA.	*ENTEROZOA.*

GRADE I. (of the Enterozoa).
ENTEROCOELA = COELENTERA.

GRADE II. (of the Enterozoa).
COELOMOCOELA = COELOMATA.

PHYLA (of the Coelomocoela).
ECHINODERMA, MOLLUSCA, APPENDICULATA, PLATYHELMIA, VERTEBRATA, etc.

CHAPTER VIII.

THE ECHINODERMA.[1]

PHYLUM ECHINODERMA.

GRADE A. PELMATOZOA.

CLASS I. CYSTIDEA.
,, II. BLASTOIDEA.
,, III. CRINOIDEA.
,, IV. EDRIOASTEROIDEA.

GRADE B. ELEUTHEROZOA.

CLASS I. HOLOTHURIOIDEA.
,, II. STELLEROIDEA.
,, III. ECHINOIDEA.

General Features.—This is one of the best characterised and most distinct Phyla of the Animal Kingdom. Nearly all the living animals included in it, such as the sea-urchin (Echinoid), starfish (Asteroid), brittle-star (Ophiuroid), sea-cucumber (Holothurian), sea-lily (stalked Crinoid), or feather-star (free Crinoid), can readily be distinguished through their possession of a radial symmetry, in which the number five is dominant, of a sub-epidermic skeleton composed of calcium carbonate, with a characteristic micro-structure resembling trellis-work, and of a system of sacs, canals, and tubes that carry water through the body, especially by means of five radial canals from which small branches called *podia* are given off to the exterior. The extinct forms known as Blastoidea and Edrioasteroidea appear to have had a similar organisation; and the same statement may be made of most of the Cystidea, another extinct class.

It is true that there are recent forms in which the quinqueradial symmetry or pentamerism is obscure; but, on the whole, it is so marked a feature that the early zoologists, and notably Cuvier, placed the Echinoderma together with the Coelentera in a subkingdom Radiata. The presence of a gut distinct from the body-cavity (*coelom*) is alone enough to mark the superiority of Echinoderm organisation, as was first insisted on by Leuckart. The resemblance of certain Holothurians to the Gephyrea is but superficial and secondary; the above-mentioned characters form sufficient distinction.

---

[1] By F. A. Bather, M.A.

Examples of the Classes.—Within the Echinoderma is great diversity of organisation. Between the worm-like, semi-gelatinous Holothurian, *Synapta*, living in the mud of the shore, and the stalked *Pentacrinus* of the depths of the sea, or the brittle-star of the rock-pools, there might well seem an impassable barrier. Taking typical examples of the various classes, let us note the more obvious differences. In an ordinary Holothurian (e.g. *Holothuria*, *Cucumaria*, Fig. IV. 4, p. 231) the body is cucumber-shaped, with a mouth at one end and an anus at the other; round the mouth is a ring-canal of the water-vascular system, and from it are given off five radial canals, running below the surface of the flexible integument and sending podia to the exterior; two of the avenues (*ambulacra*) of podia run along that surface of the body which is away from the ground and may be called "dorsal"; the "ventral" surface, containing the other three ambulacra, is often flattened to form a kind of walking sole. A Holothurian has no arms or projecting rays, but its mouth is surrounded by a circlet of tentacles, often branched, retractile at will, and serving to collect food. A Regular Sea-urchin (e.g. *Echinus*, *Cidaris*, Figs. VII., XVII. pp. 290, 303) resembles a Holothurian in being without projecting rays; but it is more spherical in shape, with a rigid test, and moves with its mouth towards the sea-floor, and with its anus at the opposite pole of the body. In a Heart-urchin (e.g. *Spatangus*, Fig. XLV. p. 324), which moves through and swallows mud and sand, the body has become obliquely elongate, *i.e.* with the long axis at an angle of 36° to the position it occupies in a Holothurian; the mouth has moved a little forward, and the anus has moved down from the top of the body to its lower surface, so that both mouth and anus lie on the under surface, at either end of the long axis. In Echinoids, the radial water-vessels are beneath the test ("hypothecal") and stretch from the oral to the anal pole. In a Starfish the mouth is in the centre of the under surface, while the anus is almost in the centre of the upper surface, but is absent in a few forms; the body, encased in a yielding theca, is either markedly pentagonal in outline or star-shaped; in the latter case a central "disc" may be distinguished from the "arms." The number of arms varies from five (e.g. *Asterias rubens*, Figs. I., IV. pp. 240, 242) to over forty (e.g. *Heliaster*). The radial water-vessels, one to each arm, lie in a groove on the oral surface ("epithecal") and are fringed by podia, which do not pass on to the aboral surface at all. An

Ophiuroid (Fig. XIII. p. 261) resembles a starfish in which there is a sharp distinction between arms and disc; the mouth is on the under surface, but there is no anus. Whereas the arms of a starfish are merely extensions of the body, containing the generative glands and processes from the stomach, those of an Ophiuroid contain only blood-vessels, water-vessels, and nerves, and, being themselves used as locomotor organs, have a stout internal skeleton of separate ossicles, worked on one another by well-developed muscles, but have less developed podia; they are nearly always five, and unbranched except in Astrophytidae (Fig. XXXII. p. 277). As is explained on p. 238, however, no sharp line can be drawn between Asteroid and Ophiuroid structure. A Crinoid (Fig. III. p. 98) differs markedly from all the forms just mentioned, in that the mouth faces upwards, or away from the sea-floor; the anus is also on the upper surface. This position is connected with the fixed habit of the Crinoids, which are attached temporarily or permanently to the sea-floor by their aboral surface, usually through a jointed stem. This fixed state of existence is correlated with the development of a jointed process ("arm" or *brachium*) from each radius of the rigid theca. The arms are often forked many times; they contain extensions of the nervous, blood-vascular, water-vascular, and generative systems, and have a ventral groove lined with cilia which sweep currents of water to the mouth. The Blastoids (Fig. IV. p. 82) may be roughly described as Crinoids without brachia, but with food-grooves on the oral surface of the theca, fringed with jointed skeletal processes (*brachiola*). The Cystidea, like the Crinoids, are fixed, with mouth and anus on the upper surface; the relations of their food-grooves and water-canals vary greatly; in some of the older ones (Fig. II. p. 44) radial symmetry does not seem to have affected even these organs, still less, therefore, any other organs of the body. The Edrioasteroidea (Fig. VI. p. 209) are sessile, with upwardly directed mouth and anus, with five food-grooves radiating from the mouth, sometimes on to the aboral surface, as in Echinoids, and apparently with hypothecal water-canals, also as in Echinoids, at any rate with some portions of the water-vessels penetrating the test along the ambulacra.

Phylogeny and Ontogeny.—The combined evidence of comparative anatomy, embryology, and palaeontology indicates that the Echinoderma owe most of their obvious characters, such as radiate symmetry, the ambulacra, and the coil of the gut, to their having passed through a "pelmatozoic" stage, *i.e.* a stage in which the animal was attached by a part of its body wall, in which the mouth, and to a less extent the other apertures, faced upwards, while there was a tendency to the radiate (pentamerous) extension of food-grooves with accompanying organs (see Chapter IX., “Pelmatozoa”). Setting aside these characters, the origin of which may be traced in individual development, and selecting those common to the early stages of all Echinoderms, zoologists have imagined a phylogenetic stage, the two-sided or *Dipleurula* stage (Fig. I.), more or less repeated in the *Dipleurula* larvae of recent Echinoderms (Fig. II.). The animal was marine. Its long axis was antero-posterior and parallel to the sea-floor. The mouth (*O*) was anterior and ventral; the anus (*As*) posterior or postero-ventral. The two were joined by an uncoiled gut, perhaps with a stomachal enlargement in the middle. On either side of this lay the coelom, formed by constriction from the larval stomach or archenteron, in other words, an “enterocoel”; it was divided into a right and left anterior portion (*a.c*), and a right and left posterior portion (*r.p.c* and *l.p.c*). Each anterior vesicle was connected with the exterior by a canal, opening at a dorsal pore (*M*) on each side the median line, sometimes, perhaps, fusing into one. These canals were indirectly connected (*s.c*) with posterior offshoots from the anterior coelom, the right and left hydrocoels (*r.hc* and *l.hc*). Gonads developed from the coelomic endothelium. The ectodermal epithelium was probably ciliated, and a portion of it in the “preoral lobe” (*p.l*) was differentiated as a sense organ, with longer cilia and underlying nerve-centre (*n*), from which two gangliated nerves ran back below the ventral surface. In the mesoblastic connective tissue, derived by the migration of cells, there was a tendency to the secretion of crystalline calcium carbonate. Except

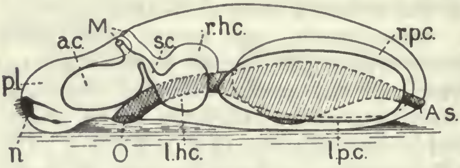


Fig. I.

Diagrammatic reconstruction of the imagined *Dipleurula* ancestor. Anterior end on left of drawing; organs of left side towards observer, and with stronger outline than those of right side. For description and lettering, see adjoining text.

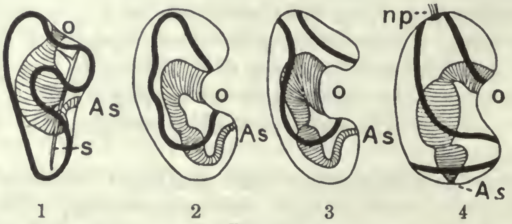


Fig. II.

Dipleurula larvae seen from right side (partly after Lang). 1, *Pluteus* of Echinoid; 2, *Auricularia* of Holothurian; 3, *Bipinnaria* of Asteroid; 4, *Tornaria* of Enteropneustan; *O*, mouth; *As*, anus; *s*, spicule; *np*, neural plate with cilia. The strong black lines represent ciliated bands; the shaded areas show the course of the gut.

for the latter character, the *Dipleurula* agrees in essentials with the larva of Enteropneusta, which was described by Joh. Müller (1850) as an Echinoderm larva, under the name *Tornaria* (Fig. II. 4).

The simplest larval form among recent Echinoderms, that of the Holothurians, known as *Auricularia* (Fig. II. 2, and Fig. III.), differs from the *Dipleurula* in being bent upon its ventral surface, so that the mouth lies in the middle of the concavity so formed, while in front of it is a "preoral lobe," and behind it is a similar prominence, in the middle of which, on the ventral surface, is the anus; the cilia are restricted to a band immediately surrounding the mouth, and a band that passes in front of the mouth, then round the edge of the ventral concavity, and across in front of the anus. In subsequent development the ciliated ring becomes very sinuous, and when the *Auricularia* assumes a barrel shape, before changing into the Holothurian, the ring atrophies in sixteen places, and the separate pieces unite in such a way as to form five rings like hoops round the barrel. In this stage the mouth has again passed up to the anterior pole, and the anus down to the posterior. This form is called the *Pupa* (Fig. I. 8, p. 219).

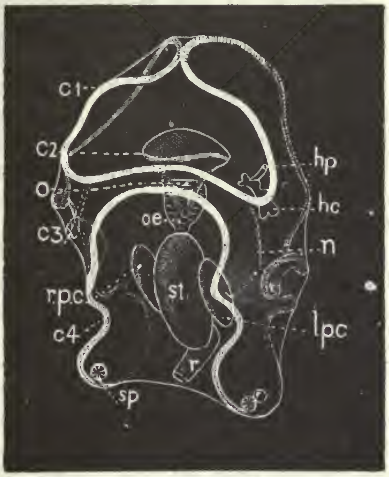


FIG. III.

Auricularia of *Synapta*, the ventral surface and left side facing the observer (after Semon). *O*, mouth; *oe*, oesophagus; *st*, stomach; *r*, rectum; *hp*, hydropore; *hc*, hydrocoel; *r* and *lpc*, right and left posterior coelom; *n*, nervous band; *sp*, spicule in form of wheel; *c*, ciliated bands, viz.—1, preoral; 2, adoral; 3, circumoral; and 4, anal. ×25.

The only free larval form that is known among Pelmatozoa is that of the highly specialised free-moving Crinoid, *Antedon*. It resembles the Holothurian *Pupa* in general shape (Fig. IV.), and in the possession of five ciliated bands (*cc*), probably derived in a similar manner; but since the early stages have been pressed out of the development, this cannot be considered proven. Here, moreover, there remains a ventral concavity, through which the definitive mouth breaks (*O*); there is no anus at this stage. Anteriorly is a tuft of long cilia.

Most Asteroidea have a larva known as *Bipinnaria* (Fig. II. 3, and Fig. VI. 10), which passes through an *Auricularia* stage. By a meeting of the sinuosities of the ciliated ring anteriorly, there is formed a preoral ring which separates from the rest. The ventral depression runs up on either side the preoral area, and eventually surrounds it and its ciliated ring. In the region of the ciliated rings the body stretches out processes, which are symmetrically paired, except the frontal process, which bears the preoral ring. In some species this process splits into three branches and the cilia disappear; such a form is called *Brachiolaria*.

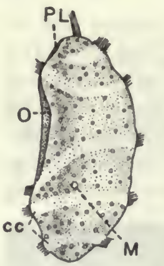


FIG. IV.

Larva of *Antedon* (after Bury). Anterior end, with preoral lobe (*PL*), uppermost. × 95.

A still further development is the *Pluteus* larva (Fig. II. 1, and Fig. V.) of Ophiuroids and Echinoids, characterised by the decrease of the preoral area and the increase of the anal area; paired processes extend forward, and an unpaired process stretches backward from the posterior end of the anal area; these processes are usually very long and supported by spicules, but movable. Two, arising from the posterior and lateral region of the ciliated ring, are pronounced in Ophiuroids but absent in Echinoids.

The development of the larval form from the ovum is effected in much the same way in all known Echinoderma (Fig. VI.). The segmentation of the ovum is total and quite or almost equal (Fig. VI. 2). A coeloblastula is formed with a segmentation cavity, and with a wall of a single cell-layer, thicker in one region (Fig. VI. 3). This region is invaginated, forming the archenteron of a gastrula (Fig. VI. 4). At about the same time the thickened region, now the end wall of the archenteron, proliferates endoderm cells, some of which wander into the segmentation cavity, where they may be joined by a lesser number from other parts of the gastrula wall (ectoderm), and so form mesenchyme, from which mesoderm tissue is ultimately developed (Fig. VI. 5). The archenteron occupies but a small part of the segmentation cavity, its lumen is usually narrow, and the external opening forms a small blastopore, which in *Antedon* soon closes. Both endoderm and ectoderm are usually ciliated from the beginning; but in *Antedon* cilia appear only on the ectoderm after gastrulation.

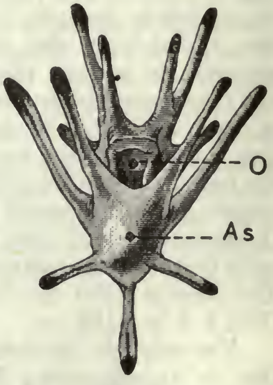


FIG. V.

Pluteus of a Heart-urchin, from ventral side (after Lang). *O*, mouth; *As*, anus.

The larva becomes bilaterally symmetrical by dorso-ventral compression and the formation of a ventral concavity. · The inner, *i.e.* anterior, end of the archenteron becomes constricted off from the rest of the archenteron to form the "coelom" (Fig. VI. 6). The coelom sends backward a process on each side in the dorsal region; the hinder parts of these become constricted off as a "right and left posterior coelom," which almost meet posteriorly; the remainder forms the "anterior coelom" (Fig. VI. 7). At the hinder end of the anterior coelom, on both the right and left side, there is a small outgrowth, the "right and left hydrocoel" (Fig. VI. 8); that on the left is, as it happens, much more developed, but the presence of a right hydrocoel has been proved by Metschnikoff (1869) and MacBride (1896), (*y* in Fig. VI. 9). Near the median dorsal line, above the hinder end of the anterior coelom, a perforation arises in a thickening of the ectoderm,

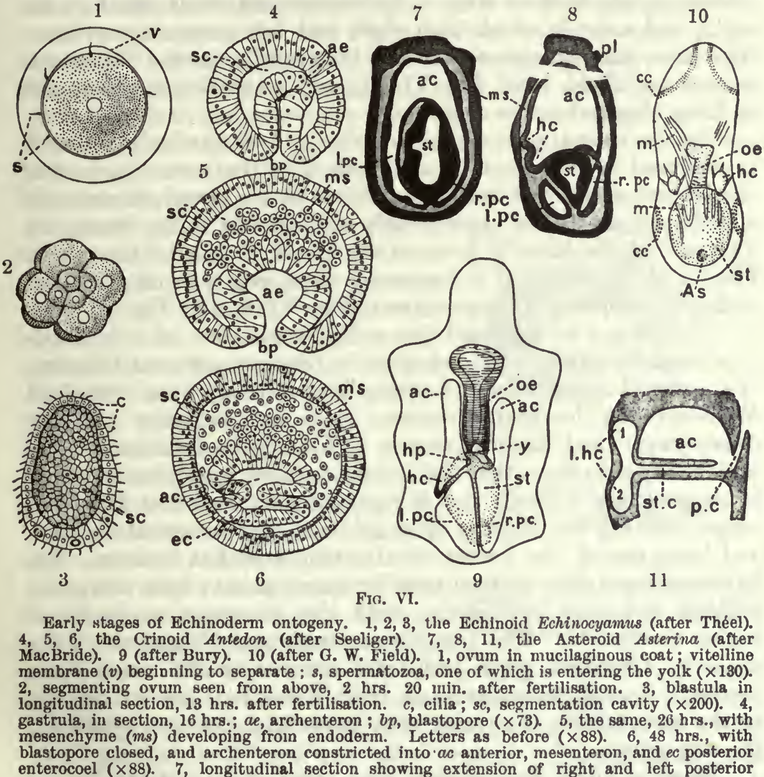


Fig. VI.

Early stages of Echinoderm ontogeny. 1, 2, 3, the Echinoid *Echinocyamus* (after Théel). 4, 5, 6, the Crinoid *Antedon* (after Seeliger). 7, 8, 11, the Asteroid *Asterina* (after MacBride). 9 (after Bury). 10 (after G. W. Field). 1, ovum in mucilaginous coat; vitelline membrane (*v*) beginning to separate; *s*, spermatozoa, one of which is entering the yolk (×130). 2, segmenting ovum seen from above, 2 hrs. 20 min. after fertilisation. 3, blastula in longitudinal section, 13 hrs. after fertilisation. *c*, cilia; *sc*, segmentation cavity (×200). 4, gastrula, in section, 16 hrs.; *ae*, archenteron; *bp*, blastopore (×73). 5, the same, 26 hrs., with mesenchyme (*ms*) developing from endoderm. Letters as before (×88). 6, 48 hrs., with blastopore closed, and archenteron constricted into *ac* anterior, mesenteron, and *ec* posterior enterocoel (×88). 7, longitudinal section showing extension of right and left posterior coeloms (*rpc*, *lpc*) from anterior coelom around larval stomach (*st*), (×60). 8, further stage, showing *rpc* and *lpc* separated from *ac*, and lobes of the rudimentary left hydrocoel (*hc*), (×60). 9, dorsal view of a *Bipinnaria*. *oe*, oesophagus; *hp*, hydropore; *y*, "blood-vascular space," Bury, perhaps rudiment of right hydrocoel. Other letters as before (×50). 10, *Bipinnaria* of *Asterias*, four days old. *cc*, ciliated band; *m*, mesenchymatous muscle fibres (×73). 11, diagram showing relations of stone canal (*stc*) and pore canal (*pc*) to left hydrocoel (*lhc*) and anterior coelom (*ac*).

forming the "hydropore" and the "pore canal"; while, in no connection with this, a groove arises along the hinder wall of the anterior coelom, and develops into a canal connecting the left hydrocoel with the anterior coelom, and called "stone canal," because its homologue in recent adult Echinoderms develops spicules in its walls (Fig. VI. 11). MacBride (1896) has observed larvae of *Asterina gibbosa*, in which there were a hydropore and stone canal on the right, and some in which both right and left pores were present. The latter arrangement occurs also temporarily in the Bipinnaria of *Asterias* (Field, 1892, Fig. VI. 10), and is that which we suppose to have obtained in the *Dipleurula*.

On the ventral side, at the anterior end of the body, a mouth is produced by invagination, and leads into the remaining part of the archenteron, which becomes modified into a larval stomach and a short rectum curved ventralwards and opening at the blastopore. The part of the larva in front of the mouth is called "the preoral lobe," and a portion of it becomes a sense organ, usually ciliated, with a development of nerve tissue (Fig. VI. 9, 10; Fig. I.).

It must not be supposed that a *Dipleurula* larva of this simple type actually exists. In each class it presents some modification, the outward appearances of which have already been described. Moreover, the internal structures vary in the order of their development and in persistence. Enough is common to the various types to show that the *Dipleurula* larva is no phantasm, and to suggest very strongly that it represents an ancestral *Dipleurula* stage, differing but slightly if at all from the ancestral *Tornaria*, and being one of the lowest of all animals with a coelom. The hydrocoels and their indirect exterior openings have been compared, perhaps not very judiciously, with the excretory nephridia of higher Coelomata. The possible connection of *Tornaria* with the ancestral Chordata gives additional interest to the resemblance between stereom formation and bone formation (see p. 29), and to the invagination of a primitively superficial nervous system in the two groups.

Between adult Echinoderms and other groups of the Animal Kingdom no comparisons are possible. From this stage onward the Echinoderm follows a path of its own. By a remarkable metamorphosis, varying in its details but presenting some common features in the different classes, the almost bilaterally symmetric larva is transformed into the almost radially symmetric adult. This metamorphosis undoubtedly represents the changes that took place in the early history of the classes; and the extraordinary difficulties of interpretation are due to the enormous compression of that history, the elimination in some cases of unnecessary stages, and the unequal acceleration of others. The clue is offered by the older fossils, which, as explained under Cystidea, forcibly suggest that all Echinoderma are descended from sessile ancestors (necessarily representing a stage subsequent to the *Dipleurula*), and that the oldest among these had not acquired radial symmetry, that being, it would appear, a consequence of fixation. Fixation was retained more or less completely by Cystidea, Blastoidea, Crinoidea, and Edrioasteroidea; but among the other classes it is only the Stelleroidea that now preserve traces of it in their ontogeny.

The passage from the *Dipleurula* to the fixed stage is best studied in *Antedon* (Bury, 1888; and Seeliger, 1893); but even here changes that, in phylogeny, must have succeeded fixation now precede it, and actually precede the free-swimming stage of the larva. Fixation takes place by a modified portion of the preoral lobe (*p.l*), as also in Stelleroidea. The phylogenetic result of this was the passage of the mouth (*O*) to the posterior end of the *Dipleurula*, which was now directed upwards (Fig. VII.). With the mouth went the hydrocoel. The attachment appears to have been towards the right side, for thus only can we account for the fact that the structures on the left of the *Dipleurula* increased at the expense of those on the right. It was therefore the left hydrocoel (*l.hc*) and stone canal (*s.c*) that moved upwards with the mouth, while those on the right disappeared. The nervous structures of the anterior end remained there or, possibly, atrophied. The forward portion of the anterior coelom (*a.c*) shared in the construction and elongation of this region; but its hinder portion was dragged up along with the hydropore (*M*) and formed the "parietal canal" (*par*), so called because it lies along the outer wall of the larva. The left posterior coelom (*l.p.c*) of the *Dipleurula* was caught in between the oesophagus and the stomach, and so passed upwards, towards what we may now call the oral pole of the fixed stage; while the right posterior coelom (*r.p.c*) was pushed downwards by the stomach pressing to the right and thus came to lie nearer the aboral pole. The blastopore is early closed in the ontogeny of *Antedon*, but we infer from the position of the larval rectum that in phylogeny the anus (*As*) did not move upwards so rapidly as the mouth. The effect of these changes was a torsion of all the structures in the upper part of the body. The gut was thrown not into a simple loop, but into a dextral coil. The pressure of the oesophagus against the hydrocoel

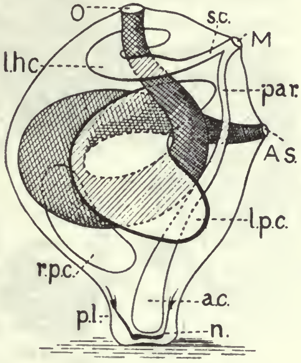


Fig. VII.

Diagrammatic reconstruction of the imagined primitive Pelmatozoic ancestor. Compare carefully with Fig. I. and with adjoining text.

not merely pulled it up, but pressed it into a horseshoe curve, with the opening directed to the anal side. The left posterior coelom was curved in like manner. The further elongation of the fixed aboral end involved lobes of the right posterior coelom and initiated their downward extension, first on the right side of the anterior coelom, then gradually curving round it. This torsion and shifting of internal organs may be compared with the simpler case of streptoneurous Gastropoda.

Careful study of the two diagrams, representing the *Dipleurula* (Fig. I.), and the primitive Pelmatozoan or fixed stage (Fig. VII.), will enable the student to appreciate the peculiar position of the internal structures in the *Antedon* larva, of which a few sections are here given for comparison (Fig. VIII.). The structure is far more complicated than in Fig. VII., owing to extensions from the coelomic cavities. In the earlier sections the hydrocoel is still

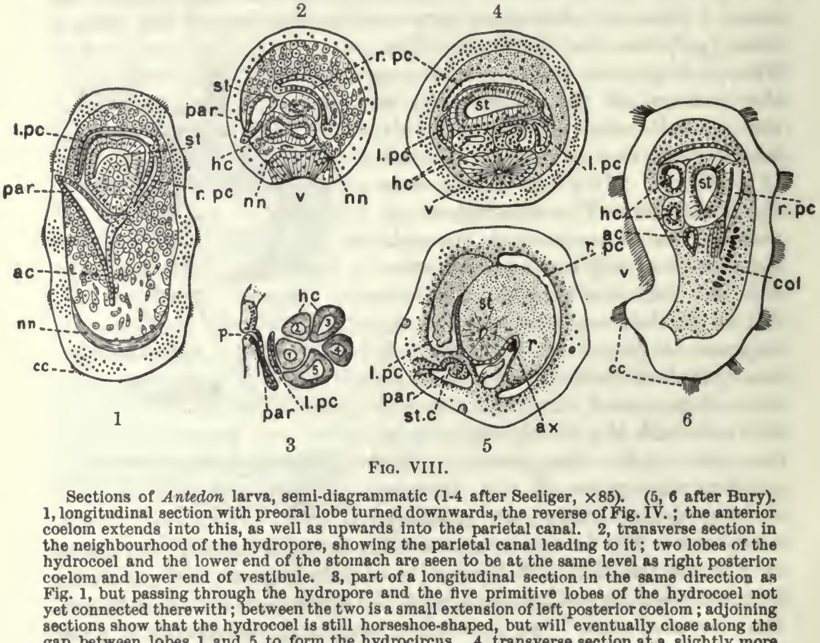


FIG. VIII.

Sections of *Antedon* larva, semi-diagrammatic (1-4 after Seeliger, ×85). (5, 6 after Bury). 1, longitudinal section with preoral lobe turned downwards, the reverse of Fig. IV.; the anterior coelom extends into this, as well as upwards into the parietal canal. 2, transverse section in the neighbourhood of the hydropore, showing the parietal canal leading to it; two lobes of the hydrocoel and the lower end of the stomach are seen to be at the same level as right posterior coelom and lower end of vestibule. 3, part of a longitudinal section in the same direction as Fig. 1, but passing through the hydropore and the five primitive lobes of the hydrocoel not yet connected therewith; between the two is a small extension of left posterior coelom; adjoining sections show that the hydrocoel is still horseshoe-shaped, but will eventually close along the gap between lobes 1 and 5 to form the hydrocircus. 4, transverse section at a slightly more orad level than in 2, and in an older larva; the vestibule is here closed over; note the mesenteries between right and left posterior coeloms. 5, transverse section of an older larva, in which the vestibule has passed right up to the oral pole, and a rectum (*r*) has formed; between this and the stomach is seen the rudiment of the axial organ; the parietal canal remains, but the stone canal now opens into it (×125). 6, median longitudinal section, the vestibule still open, columnals forming around extensions of right posterior and anterior coeloms; left posterior coelom is seen above the stomach as a lobe of the hydrocoel (×120).

Explanation of letters—*ac*, anterior coelom; *ax*, axial organ; *cc*, ciliated bands; *col*, columnals; *hc*, hydrocoel; *l.pc*, left posterior coelom; *nn*, nerves; *p*, hydropore; *par*, parietal canal; *r*, rectum; *r.pc*, right posterior coelom; *st*, stomach; *st.c*, stone canal; *v*, vestibule.

on the aboral side of the right posterior coelom; indeed, the mouth itself is not at the future oral pole, for the larval mouth closed early, and the place where it was became arched over by lips of ectoderm, which formed a "vestibule" (*v*). This vestibule it is that gradually moves up; a fresh mouth ultimately breaks through into it, and the lips again unfold at the new oral pole. The connection of the anterior coelom, through the parietal canal and the hydropore, with the exterior, persists (cf. Fig. VIII. 1 and 3); the hydrocoel opens into the parietal canal by the stone canal at a later period (Fig. VIII. 5).

There is reason to believe that some of the early Cystidea (Amphoridea, p. 43) had an internal structure scarcely more advanced than Fig. VII. But the fixed stage had further effects. The most notable was the prolongation of ciliated and tentaculiferous grooves from the mouth, accompanied by processes from the hydrocoel. At first there were three such radial extensions: anterior, right, and left, since the presence of anus and hydropore, and the absence of hydrocoel on the posterior side prevented extensions in that direction (Fig. IX.). The five rays, so characteristic of Echinoderma, were produced by the forking of the right and left rays. It was only at a later date, when the hydrocoel had grown into a ring round the oesophagus, that the five rays could proceed equally from this ring. The division of the rays into a pair enclosing anus and madreporite, and known as the *bivium*, and the three others (anterior, right ant. and left ant.), known as the *trivium*, is opposed to this fundamental structure. It must further be noted that this bilateral symmetry of the rays has nothing to do with the bilateral nature of the *Dipleurula*.

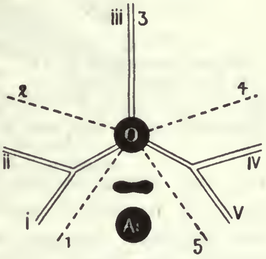


Fig. IX.

The pentamerism of Echinoderma contrasted with a regular pentamerism. *O*, mouth; *As*, anus; between them is the madreporite. 1, 2, 3, 4, 5 are the rays of an imaginary perfect pentamerism, of which 1 and 5 are the *bivium*, 2, 3, 4, the *trivium*. i, ii, iii, iv, v are the five rays of a Pelmatozoan.

While these changes were in progress the formation of stereom continued. At first there were only spicules deposited in the mesenchyme (see Fig. II. 1, and Fig. III.). These enlarged and fused into plates, which eventually became so large as to abut on one another. These plates were arranged in the mesoderm beneath the ectoderm. An account of their arrangement and structure will be found under Amphoridea (p. 45). Through the fixation below and the radiation of the hydrocoel and food-grooves above, these plates gradually came to lie in definite positions and to assume a definite number, shape, and size. The ontogeny of *Antedon* suggests their division into two groups (Fig. X.): one formed around the upper, oral coelom (*l.pc*, *i.e.* the left posterior coelom of the *Dipleurula*), which gradually encircled the oesophagus; the other around the lower, aboral, or apical coelom (*r.pc*, *i.e.* the right posterior coelom of the *Dipleurula*). The former set were affected by radiate symmetry before the others, and in *Antedon* larva are represented by five large plates, the "orals" (*O*). The latter set form the plates of the aboral side of the adult Echinoderm. In a Pelmatozoan they form the dorsal cup (*B* and *IB*) and the ossicles of the stem (*col*) when that organ is present.

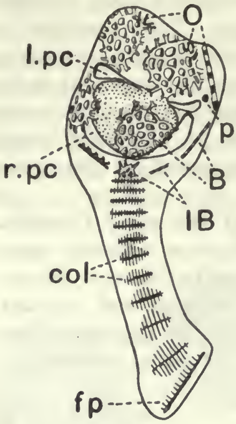


Fig. X.

Skeletal development in *Antedon* larva (after Seeliger). *p*, hydropore; *fp*, fixing plate of stem, "dorso-central"; for other letters, see adjoining text. × 66.

We have now traced the history of the Echinoderma up to a form fixed aborally, and with rays, normally five in number, proceeding from the mouth and underlying the hydrocoel ring or *hydrocircus*. These rays involved other of the internal organs, notably portions of the oral and aboral coelom, and accompanying them was a development of epithelial nerves and a circumoral nerve ring. The dividing wall between the right and left posterior coeloms, the dorsal mesentery of the *Dipleurula*, now lies horizontally or transverse to the long axis. A new vertical mesentery, both above and below, is formed by the tissue separating the incurved ends of the oral and apical coeloms respectively. On the inner walls of these coeloms, adjoining this mesentery, is a thickening of the endothelium (*ax* in Fig. VIII. 5), to form eventually a strand passing up to the main axis through the coil of the gut, and known as the "axial cord." This, in the adult, originates the gonads, which seem at first to have been expelled through an aperture in the body wall between mouth and anus, as seen in Holothurians and some Cystidea. Subsequently this becomes involved in the radiate symmetry.

The phylogenetic stage thus reconstructed on the evidence of embryology and palaeontology corresponds on the whole to the stage imagined by Semon (1888), and named by him *Pentactæa* (five-rayed). The question arises: How far does this represent the ancestor of all Echinoderms? There can be no doubt that this actually was a stage in the history of the fixed Echinoderms (Pelmatozoa); that it was also a stage in that of the free Echinoderms (Eleutherozoa), is coming more and more to be the opinion of zoologists. The development of *Asterina* indicates the possible relation between those two groups. Here MacBride (1896) has shown that the larva is early attached by the preoral lobe, and that it bends over on this so as to bring the mouth downwards. The internal structures do not, however, undergo that complete translation and torsion which occur in the Crinoid. Traces of it are seen in the greater development of the left hydrocoel and left posterior coelom. Fig. XI. attempts to show what would happen in the case of a primitive *Pentactœa* that bent over in this way; while the mouth passed down, the anus and hydropore would tend to remain on the upper surface, where they could best fulfil their functions. In the present ontogeny of the Asteroid, the development is direct from the *Dipleurula* to this stage, the intermediate steps imagined for the phylogeny being omitted as unnecessary.

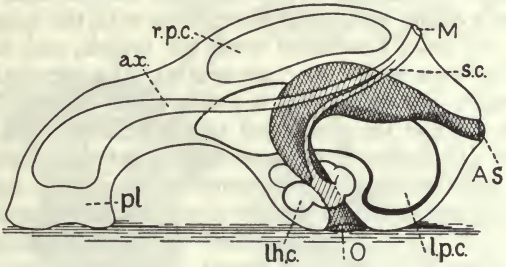


FIG. XI.

Change from *Pentactœa* to Stelleroid type. *O*, mouth; *As*, anus; *M*, madreporite; *r.p.c* and *l.p.c*, right and left posterior coelom; *l.hc*, left hydrocoel; *s.c*, stone canal; *pl*, preoral lobe; *ax*, axial sinus, remains of anterior coelom.

But to those phylogenetic steps are due the peculiar positions assumed by the left hydrocoel and left posterior coelom, as well as the radial folding which they undergo. Study of Fig. XI. will elucidate the complicated internal arrangement of the developing *Asterina*. Further flexure causes the ends of the curved hydrocoel to grow around the stalk, which thus deceptively appears to spring from the oral surface, not from the aboral as in Crinoids. Subsequently the stalk atrophies, and the young starfish is a free-moving form, with mouth on the sea-floor, with anus and madreporite directed upwards, and with the beginnings of five arms containing extensions of the left hydrocoel, of the oral coelom (derived from l. post. coelom), and of the stomach (Fig. XII.). During development the larval mouth and anus are closed, and break through again in their adult positions; this points to a migration of those openings during phylogeny, which migration cannot well be repeated in ontogeny.

A vast amount of discussion has taken place over the question whether the plates of the Crinoid calyx find homologues in other

Echinoderma. The orals on the one side are supposed by some (*e.g.* Lovén, P. H. Carpenter, Sladen) to be represented by somewhat similarly situated plates in Stelleroidea ("buccal shields" of Ophiuroids, "odontophores" of Asteroids), and by a circumoral calcareous ring in Holothurians. The plates of the dorsal cup have been homologised with plates very similar in shape and arrangement that are often to be observed in Stelleroidea, notably on the aboral side of the compact body of Ophiuroids, and with two circlets of plates at the aboral pole of Echinoids. It has been supposed that all Echinoderma primitively possessed a definite calycinal system, thus composed: a central aboral plate ("dorso-central"), five plates surrounding this ("basals," "genitals" of Echinoids), five plates following on these and alternating with them ("radials," "terminals" of Asteroids, "oculars" of Echinoids); these together formed the "apical system," and to them was sometimes added a circlet below, and alternating with, the basals ("infra-basals"): five orals, alternated with the radials, and to these P. H. Carpenter once added an "oro-central," the correlative of the dorso-central. The oro-central is a discredited myth. The dorso-central is a plate at the distal end of the Crinoid stem, *i.e.* in the preoral lobe (*fp* in Fig. X.); there is no proof that it ever formed part of an apical system, and it cannot be considered either homogenetic or homoplastic with the aboral central plate sometimes seen in Stelleroidea. As for the basals and radials of the Crinoid, they are, as stated above, formed around the right posterior coelom; this also is the position of their supposed homologues in *Asterina* (Fig. XII.), and MacBride's argument that their relations to the stem are different, does not seem fatal to the above theory. What is fatal is the conclusion to which the evidence of fossils forces us—that the free Echinoderms, if they arose from stalked forms at all, indubitably did so ages before a calycinal system had been evolved. Even among stalked forms it appears that regular apical systems arose independently in different lines of descent. If, however, it be impossible to regard the apical systems of Echinoidea and Stelleroidea as homogenetic with that of Crinoidea, there can be no objection to the statement that similar plates are developed in a similar position with regard to the fundamental anatomy, under the influence of somewhat similar causes.

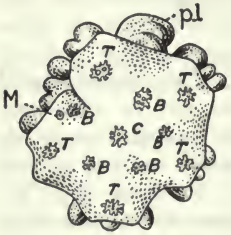


Fig. XII.

Dorsal, *i.e.* aboral, view of *Asterina gibbosa*, ten days old (after Ludwig). Shows preoral lobe (*p.l*) now on oral side; rudiments of five arms marked by five terminal plates (*T*); alternating with these are five basals (*B*); and at *C* is the so-called dorso-central; *M*, madreporite. ×56.

The Asteroids were probably the last group to branch off from the fixed Echinoderms. Hence it is that they retain many features of the *Pentactœa*, together with epithelial nerves on the floor of the arm-grooves, as in Pelmatozoa. The Ophiuroids are, as explained under Stelleroidea, scarcely to be distinguished from Asteroids. Whether they branched off at an earlier date or no is uncertain; at any rate, they have progressed farther from the *Pentactœa* type, in so far as the radial nerves have sunk below the surface and are covered by "epineural canals," which probably represent closed food-grooves (Fig. XIII. 1 and 2).

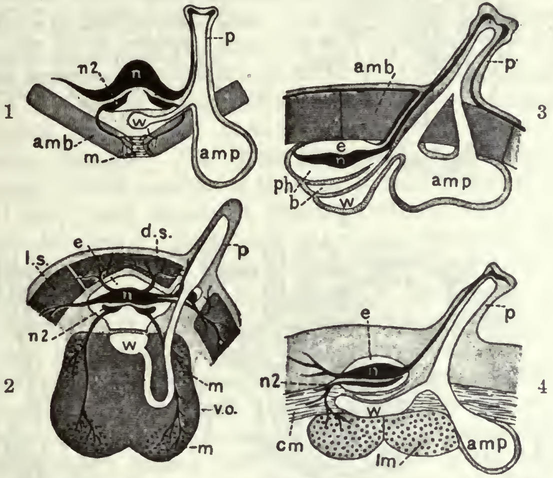


Fig. XIII.

Sections across ambulacra of—1, Asteroid; 2, Ophiuroid; 3, Echinoid; 4, Holothurian. *amb*, ambulacral ossicle; *amp*, ampulla; *b*, radial blood-vessel; *cm*, circular muscles; *d.s*, ventral scute; *e*, radial epineural canal; *lm*, longitudinal muscles; *l.s*, lateral scute; *m*, muscles; *n*, radial nerve of superficial oral system; *n*2, radial nerves of deeper oral system; *p*, podium; *ph*, pseudhaemal canal; *v.o*, vertebral ossicle; *w*, radial canal of the water-vascular system.

The development of Echinoidea has been studied by J. Müller (1852), Agassiz (1864), Metschnikoff (1869), Bury (1889), and many others. The results are summarised by Théel in his admirable account of the development of *Echinocyamus pusillus* (1892). Up to the stage corresponding to the *Dipleurula* no important divergences are manifest. The peculiarities of the ensuing metamorphosis appear due to the extreme development of a free-swimming *Pluteus* (Fig. XIV.). At an early stage there is an invagination (*am*) of the ectoderm on the left side between the bases of the ventral and dorsal posterior processes of the *Pluteus*. The inner end of this sac grows towards the left hydrocoel, while its opening nearly or quite closes (Fig. XV. 1). The five primitive lobes of the hydrocoel grow up into the floor of this sac (Fig. XV. 2), which thus serves as a kind of amnion in which the young sea-urchin is formed (Fig. XV. 3), until the size of the

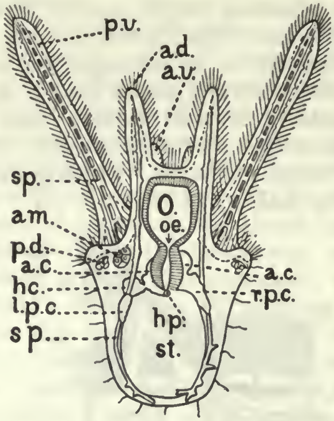


Fig. XIV.

Pluteus of *Echinocyamus* (after Théel). About 75 times nat. size.

Explanation of letters to Figs. XIV. and XV.—*a.c*, anterior coelom; *a.d*, anterior dorsal arm; *am*, amniotic invagination; *a.v*, anterior ventral arm; *hc*, hydrocoel; *hp*, hydropore; *l.p.c*, left posterior coelom; *O*, mouth; *oe*, oesophagus; *p*, podia; *pd*, posterior dorsal arm; *p.v*, posterior ventral arm; *r.p.c*, right posterior coelom; *s*, spines of Echinoid; *sp*, spicules of *Pluteus*; *sp′*, the same being absorbed; *st*, stomach.

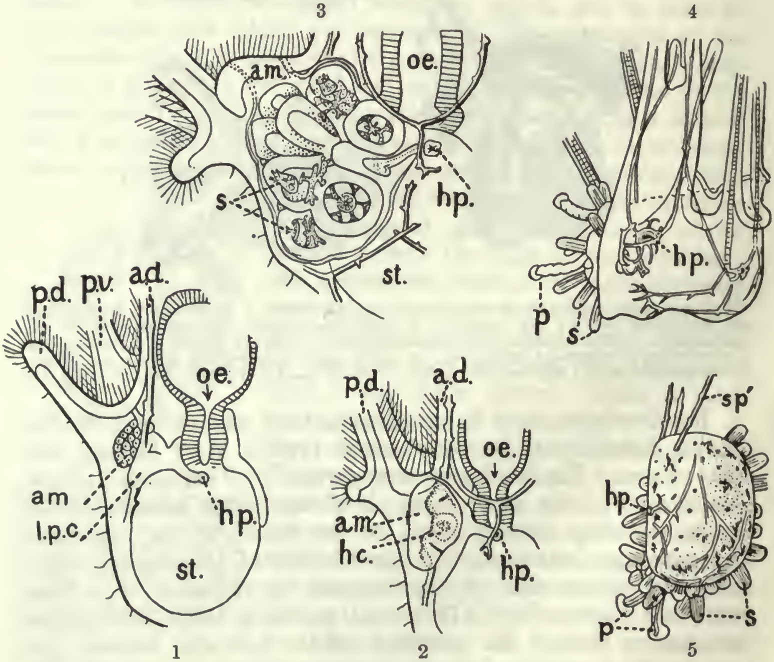


Fig. XV.

Development of *Echinocyamus* (after Théel). 1, portion of a *Pluteus* rather more developed than in Fig. XIV.; the ectodermic invagination has grown in towards the left coelom, which is now separating into a posterior portion and a hydrocoel. 2, portion of a *Pluteus* about twelve days old, showing the lobes of the hydrocoel growing into the amnion. 3, the same considerably more advanced; spines begin to develop and the amnion is connected with the exterior. 4, a *Pluteus* forty-five days old, with spines and podia of the young urchin protruding from the amnion. 5, the young urchin, bearing on its back the remains of the *Pluteus* spicules and integument (×100).

growing tube feet and spines causes it to break through the outer wall (Fig. XV. 4). While this takes place the spicular skeleton of the *Pluteus* is absorbed, and the body of the *Pluteus* shrinks up to a sac on the aboral side of the young Echinoid (Fig. XV. 5). The hydropore from the first opens on the dorsal surface, which becomes the aboral side. The right posterior coelom is also under here, as in Stelleroids. The larval stomach becomes that of the adult, but a fresh mouth is formed in the centre of the hydrocircus, while the anus is a fresh formation at the aboral pole.

It is easy to understand that, with this amniotic development in the body of the larva, most of the traces of the *Pentactœa* stage have disappeared. There is, however, evidence of a preoral lobe, while the coil of the intestine and the radiate structure of the hydrocoel, nerves, and gonads, bear witness to antecedent phylogenetic changes. On those changes light is thrown by palaeontology, which teaches us that the primitive Echinoid had a spheroidal body, with muscular, flexible walls, in which irregular plates were developed; the mouth was at the centre of the lower surface; the anus on the upper surface, and near it the madreporite (the successor of the hydropore). Combining with the evidence from fossils that from comparative anatomy, we infer that the gut had a simple dextral coil; that the oesophagus was surrounded by three rings—water-vascular, blood-vascular, and nervous; and that from each ring five branches passed up the inside of the body wall to the aboral pole; that branches from the radial water-vessels passed, between the plates in the body wall, to the exterior, and became suckers assisting locomotion, the complete structures being ambulacra; that gonads were five, unpaired, and interradially disposed in the body cavity. Such a form had lost the stem of the *Pentactœa*, and had never possessed an apical system of plates. It had, however, already developed food-grooves, with nerves and ambulacral vessels, while there must have been some radiate arrangement of the gonads. The sinking of the nerves and closure of the food-grooves forming epineural canals (Fig. XIII. 3) probably took place as we suppose it to have done in Ophiuroids. Among Pelmatozoa, the Edrioasteroidea (p. 205) present a structure removed from that of the primitive Echinoid in little but the upward position of the mouth and (probably) the madreporite, and the functional food-grooves; the notable point about the latter is the presence of openings between the flooring-plates, apparently for the passage of processes from the radial water-vessels.

The peculiarities in the structure and development of the Holothurians may perhaps be ascribed to their having in many respects regressed from the Pelmatozoic towards the *Dipleurula* type (Fig. XVI.). Thus the mouth has again come to lie at one end of the body, while the anus is at the other. With the mouth has gone the genital pore; and the madreporite, though unconnected with the exterior in the adult of most now living, must have moved towards this end also. But there is an important difference between this and the *Dipleurula* in the coil of the gut, and the vastly altered relations of the coelomic cavities with their intervening mesenteries. The arrangement indicates that the mouth, hydrocoel, madreporite, and associated organs of a *Pentactæa* gradually moved anteriorly away from the anus, thus coming nearer to the stem (preoral lobe of larva) and lengthening the gut by another half-coil. When the fixed existence was given up and the food-grooves closed in, leaving the external podia from the water-vessels, then the rays were able to extend equally in all directions from mouth to anus. The anterior ray and the two adjoining rays had thus come to be on that side of the elongate body which was directed towards the sea-floor, and to this they clung, or on it they crawled, by suckers which developed on the podia, which thus became "tube-feet." The left and right posterior rays ran along the upper surface of the body, forming the bivium of the Holothurian, homologous with the bivium of the Pelmatozoa, as shown by the position of the hydropore.

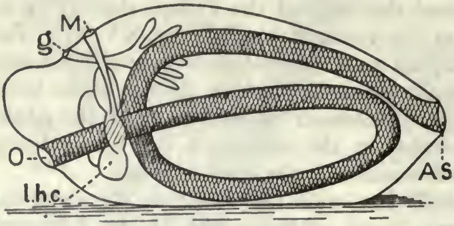


Fig. XVI.

Diagrammatic reconstruction of the imagined primitive Holothurian type, for comparison with Figs. I., VII., and XI. *O*, mouth; *As*, anus; *M*, hydropore; *l.hc*, left hydrocoel; *g*, genital opening.

The view has been held that the Synaptidae, with their simple structure and straight antero-posterior gut, represent the simplest and most ancestral Echinoderms. But if the above account be correct, this simplicity is only apparent, and is the result of regressive changes. Such is the view that now finds general favour. The *Pentactula* stage (Fig. XVII.), in the development of *Synapta*, with five interradial circumoral tentacles, slightly curved gut, and aboral anus, is therefore not the modern ontogenetic representative of the phylogenetic *Pentactæa*, as Semon supposed.

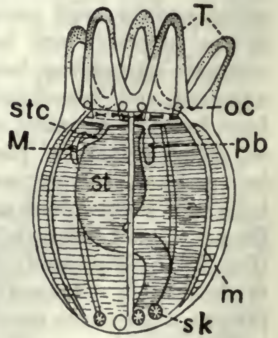


Fig. XVII.

Pentactula stage of *Synapta* (after Semon). *T*, tentacles; *M*, madreporite; *stc*, stone canal; *st*, stomach; *oc*, supposed otocysts; *pb*, Polian vesicle depending from hydrocircus; *m*, longitudinal muscles; *sk*, calcareous spicules. × 36.

Further, if our present theory be correct, we must suppose that the larval history of the Holothurians has been exceedingly compressed; so that, to take but one point, the development of the straight larval gut into the coiled gut of the adult takes place, not by migration of the mouth and associated organs, but by lengthening and twisting of the gut itself. It is noteworthy that the two lateral radii of the trivium with their nerves and muscles and tube-feet, as well as the oral tentacles to which they eventually give rise, develop much more slowly than the three other radii. Those are the three radii which are assumed in the above account to be homologous with the original three radii of the primitive Pelmatozoan (cf. Fig. IX.).

It therefore appears that the Holothurian stock branched off from the Pelmatozoa before complete pentamerous symmetry of the hydrocoel and associated organs had arisen, before any definite calycinal system had developed, while the gonads were still a simple strand opening to the exterior by a single posterior gonopore. The diminution of the skeletal elements did not favour their preservation as fossils. Their spicules indeed are found in the rocks from at least the Carboniferous downward, but if we except the problematic *Sphaerites*, Quenstedt (1852, *non* Dufts), no fossil Holothurian is known. The class was perhaps an early offshoot from the Edrioasteroidea. This theory explains how it is that the Holothurians are primitive in so many characters, although the most specialised in others; they are primitive as regards Pelmatozoic structure, specialised as regards Eleutherozoic.

Symmetries.—The radial symmetry due to the fixed phylogenetic stage is usually pentamerous. Hexamerous symmetry was independently acquired by some Cystidea. Variation from pentamerism may arise suddenly (discontinuous meristic variation of Bateson), producing hexamerous or tetramerous individuals, or species, or genera, according as the sport becomes fixed. There may also be a duplication, or further multiplication of radii, as in the ten-rayed *Promachocrinus*, or an intercalation during growth, as in the many-rayed *Labidiaster;* this is a different thing from the branching of a radius, such as occurs in Crinoids, Astrophytidae, and elsewhere. Again there may be variation by gradual atrophy of one or more radii, as in Calceocrinidae, and some heart-urchins and Holothurians. In spite of these variations, it is generally possible to divide the body of an Echinoderm, by planes passing through the ambulacra from the long or main axis, into approximately corresponding portions, "antimeres," normally five. These planes mark the radii, or better *perradii*, since the terms ray and radius have been used loosely. Organs bisected by them are "perradial"; such are invariably the main ambulacral vessels, the arms of Stelleroidea and brachia of Crinoidea, with their included organs.

Half-way between the perradial planes are the planes marking the *interradii.* Organs bisected by these are "interradial"; such are the interambulacral areas of the test, the oral plates of Crinoidea, the gonads of Echinoidea. Between the perradii and interradii are *adradii,* a term little used in practice; thecal plates adjoining the ambulacrals are called "adambulacral." In a regular pentamerous Echinoderm an interradius is opposite to a perradius, and an adradius opposite to an adradius.

All Echinoderms have a bilateral symmetry. Primitively the plane of symmetry, the sagittal plane, is determined by the mouth (anterior), the anus (posterior), and the hydropore (dorsal). But, in the first place, this sagittal plane, when clearly shown, is not the same as the sagittal plane of the *Dipleurula.* In Pelmatozoa it certainly is not; in Holothurians it only approximates to it. Secondly, in Echinoidea and some Cystidea, and in such Asteroidea as have an anus, the plane passing through the vertical axis and the madreporite (*M* plane) is not the same as that passing through the vertical axis and the anus (anal plane). Thirdly, the relations of the anal plane to the *M* plane and to the radii may vary even within a single class, *e.g.* Echinoidea and Cystidea. Consequently the selection of any one plane as a plane of orientation for the different classes is arbitrary. Also it is convenient. We take then the *M* plane and note that the hydropore lies in an interradius with a radius opposite to it (Fig. XVIII.). That radius we denote by *A*. Then placing the animal with its mouth upwards and going round the test in the direction of the watch-hand (*i.e.* dextrally), we denote the other radii in order, *B, C, D, E*. The hydropore lies in interradius *CD*. In a developing Holothurian, or in such Holothurians as retain an external madreporite (Fig. XVIII. 3), the anus and mouth both lie in the *M* plane, forming the poles of the long axis, while radius *A* bisects the ventral surface; this therefore is the sagittal plane of bilateral symmetry, and Cuénot, 1891, calls it the "Holothurian plane." In a Crinoid (Fig. XVIII. 1), anus, mouth, and aboral pole, all lie in the *M* plane, which here also is the sagittal plane; but the anus, in interradius *CD*, never marks the aboral pole of the main axis, though it may usurp the place of the mouth at the upper pole. Many Cystids, and apparently the Blastoids, have a similar orientation. Other Cystids differ in that the anus lies to left or to right of the hydropore, while the relation of the radii to the *M* plane is not clearly defined. In *Echinocystis* (p. 301), which probably represents the relations in the primitive Echinoid, the symmetry remains as in Pelmatozoa; while the mouth is at one pole of the main axis, the anus lies in or near the *M* plane, which is therefore the sagittal plane, but the madreporite is near to the aboral pole. In later Echinoids the case is altered (Fig. XVIII. 4); the first step appears to have been the passage of the anus to the aboral pole, the madreporite remaining eccentric and marking interradius *CD*; whether this *CD* is identical with *CD* of *Echinocystis*, is another question; then the anus moved away from the pole in the direction of radius *B*, so that the anal plane made an angle of 72° with the *M* plane. This new plane (interradius *DE*, radius *B*) is termed by Cuénot the "Echinid plane"; Lovén (1884) has shown that the plates of the five interradii in Echinoidea are disposed symmetrically with reference to this plane. The sagittal plane of many other sea-urchins, notably the heart-urchins and their allies (Fig. XVIII. 5), *i.e.* the plane passing through mouth, anus, and apical pole, corresponds with neither the *M* plane nor the Echinid plane, but passes through radius *D* and interradius *AB*; Cuénot calls it "Lovén's plane." The bivium (*AB*) and trivium (*C*, *D*, *E*) of a heart-urchin are therefore in no way identical with those parts in a Holothurian, a Crinoid, or a Stelleroid. In those starfish that have an anus (Fig. XVIII. 2), that organ, as shown by Ludwig, is in interradius *BC*; this with the vertical axis marks the "Asterid

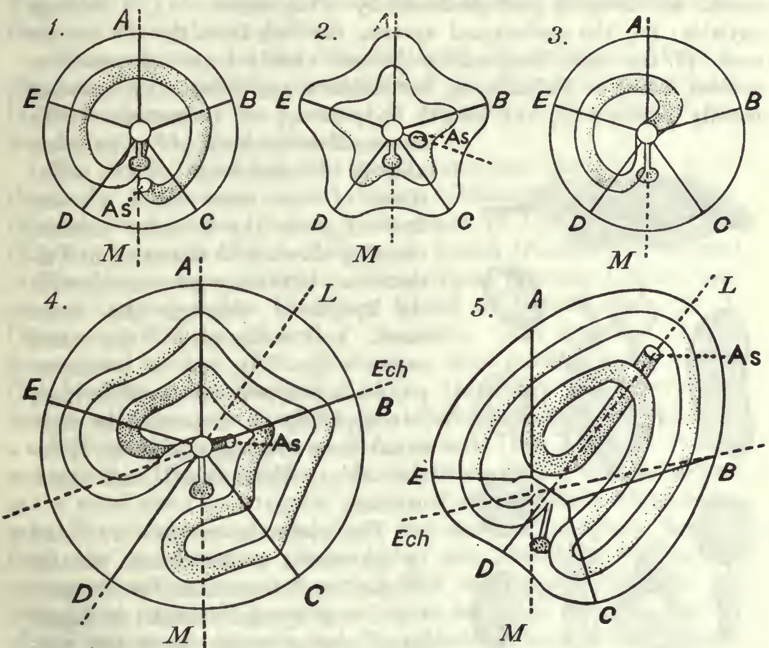


Fig. XVIII.

Planes of symmetry in Echinoderma (partly after Cuénot). 1, Crinoid; 2, eroid; 3, Holothurian; 4, Regular Echinoid; 5, Irregular Echinoid. *As*, anus; *M*, plane passing through madreporite; *Ech*, Echinid plane; *L*, Lovén's plane. For other letters, see adjoining text.

plane" of Cuénot. It is scarcely worth while to describe yet other divergences of the sagittal plane from the *M* plane, such as occur in Cystidea and Blastoidea. All of them are due to the imposition of a tertiary bilateral symmetry, obscuring the previously existing secondary bilateralism that had already replaced the bilateralism of the *Dipleurula*.

Cavities and their Contents.—The cavities into which the thecal cavity is divided by the ontogenetic changes above described, are:—(1) Gut and appendages, derived from the archenteron, with mouth and anus in part produced by invagination. (2) Coelomic cavities: (*a*) the ambulacral system, derived from the left hydrocoel; (*b*) the main body-cavity derived chiefly from left posterior coelom, which in Pelmatozoa, Stelleroidea, and Echinoidea becomes mainly adoral; (*c*) the aboral body-cavity of Pelmatozoa (with columnal extensions), of Stelleroidea, and of Echinoidea; (*d*) the axial sinus of the same three classes, derived from the anterior coelom, running down into the stem in Pelmatozoa, indirectly connected with the hydrocoel through the stone canal, and containing "the axial organ" (p. 23); (*e*) a perioesophageal sinus, sometimes subdivided, is completely or incompletely separated from (*b*), especially in Holothurioidea, Echinoidea, and Ophiuroidea.

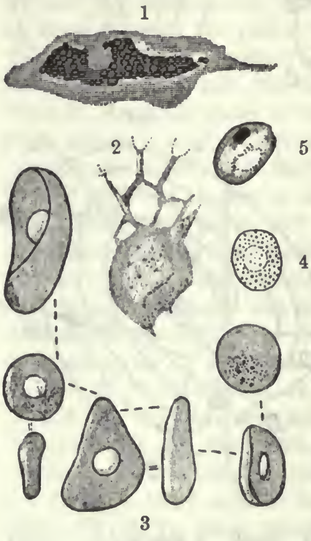


Fig. XIX.

Corpuscles of the coelomic fluid. 1 and 2 from the Echinoid, *Echinus sphaera* (after Geddes). 1, amoeboid corpuscle with granules of brown ferruginous pigment, perhaps respiratory. 2, amoeboid white corpuscle with reticular pseudopodia. 3, from the Ophiuroid, *Ophiactis virens* (after Foettinger); corpuscles of various shapes, with red colour supposed due to haemoglobin. 4 and 5 from the Holothurian, *Thyonella gemmata* (after Howell). 4, white corpuscle. 5, oval, nucleate, biconvex corpuscle, coloured red by haemoglobin. All much magnified.

The coelomic cavities are lined by pavement endothelium, usually ciliated, and sometimes further provided with special ciliated or flagellated organs which keep the contained fluid in motion (*e.g.* "urns" of Synaptidae (Fig. V. 4, p. 233); "ciliated cups" of Crinoid arms, especially pinnules; free flagellate cells of Echinoidea). The fluid is similar to that found in the lacunar "blood-vascular system"; it is sea-water, perhaps taken in through the madreporite, containing a variable amount of albumen in solution, especially in the lacunar system, and sometimes slightly yellowish or reddish. In it float various bodies, viz. (*a*) amoebocytes (Fig. XIX. 1, 2, 4) capable of wandering through all the tissues, including the skeletal, and containing refringent granules, proteids, fat, and a yellow pigment called "echinochrome" (MacMunn, 1885); they seem to be specialised as bearers of reserve food, as calcigenous cells (p. 28), as phagocytes, and as bearers to the exterior of waste products often pigmented (Durham, 1891, St. Hilaire, 1897); (*b*) red corpuscles with haemoglobin (Foettinger, 1880), non-nucleate, but vacuolate or granular in water-vessels of Ophiuroids (Fig. XIX. 3), nucleate in various coelomic cavities of Holothurians (Howell, 1886; Cuénot, 1891, Fig. XIX. 5); the respiratory nature of these is demonstrated by their containing haemoglobin.

Whatever may be the homologies of the hydrocoel, there is, physiologically speaking, no nephridial or other excretory system in Echinoderma. The function is probably performed by the wandering cells just mentioned.

The Axial Organ has had many functions ascribed to it, as shown by its various names: Heart (Tiedemann), Pseudo-heart, Central Blood-plexus (Ludwig), Glandular or Chromatogen organ (Hamann), Lymph Gland, Madreporic Gland (Koehler), Collateral or Plastidogen organ (Perrier), Ovoid Gland (Perrier, Cuénot, and others), Genital stolon, Plexiform Gland or Dorsal organ (P. H. Carpenter), Kidney (P. and F. Sarasin). The Sarasins (1888) give a good account of the literature; later notes of value are by Cuénot (1891) and Durham (1891). Generally it is a brownish, finely lobed, often pear-shaped body, showing under low magnification a complicated arrangement of tissue strands (Fig. XX. 1). It does not occur in Holothurioidea. In the other classes it is developed in the axial sinus by irregular growth of endothelium, which forms canal-like strands separated from one another by spaces derived from the axial sinus; these latter are therefore primitively connected with the water-vessels and madreporite through the stone canal. Strands growing out at an early age from the central plexus become the gonads, but the connection may be lost in later life. In association with the genital strands are also radiating "haemal strands," not true blood-vessels, but serving for the transmission of nutrient cells. Such cells, as well as pigmented, excretory amoebocytes, are found in quantity in and about the axial organ. In Pelmatozoa the axial organ, surrounded by the axial sinus and the lobes of the chambered organ, stretches right down the stem (Fig. XX. 2). The position of the axial sinus with regard to the gut suggests that nutrient fluid passes by osmosis into the axial organ, which thus serves as a kind of distributor, but there is no evidence of pulsatile pump-action, *i.e.* it is no heart. The evidence of new cell-formation is too slight to warrant the idea that the axial organ is a factory of amoebocytes. There is still room for study of this peculiar body, especially through experiment.

The Genital Organs throw light on the axial organ, since it exists only in those classes in which the gonads are affected by radiate symmetry, and not in the Holothurians. It follows that the axial organ was a secondary development. Ontogenetically the genital strands bud off from one end of it, where a ring is formed, and with the extensions of these go also extensions of the axial sinus (Fig. XXI.). The single gonad of the Holothurioidea, connected with the dorsal mesentery, appears therefore to be the homologue of the axial sinus and organ rather than of any one of the interradial gonads of the other classes. The gonads, therefore,

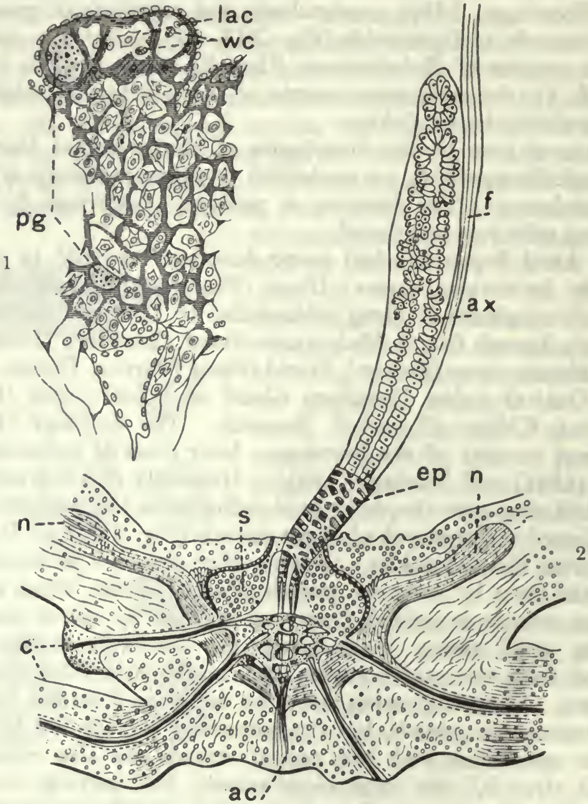


FIG. XX.

The axial organ. 1, longitudinal section through part of the organ in the sea-urchin, *Sphaerechinus granularis* (after Leipoldt). × 350. *pg*, pigment masses; *lac*, peripheral blood lacunae of the organ; *wc*, wandering cells. 2, longitudinal section, showing relations of the organ to the chambered organ in young *Antedon* (after Perrier). *ax*, cells of axial organ; *f*, fibrous membrane, which partly envelopes it; *ep*, epithelial coat continuous with chambered organ; *s*, septum of chambered organ; *n*, nerves proceeding from fibrillar envelope of same; *c*, cirri, one just budding out; *ac*, atrophied axial canal of stem, continuous with axial organ.

are of endothelial origin. There appears, however, as shown by Hamann, to be a migration of the actual sexual cells; and the view of Cuénot that these are primarily amoebocytes derived from the axial organ suggests their possible mesodermic nature. Compare the migration of sexual cells derived from the ectoderm in Hydroids. The growth and minute structure of the ovum have been described by Crety (1894), of the spermatozoon by Field (1895); both authors refer to preceding literature. No striking peculiarity is presented by Echinoderm gonads (cf. Fig. VI. 1).

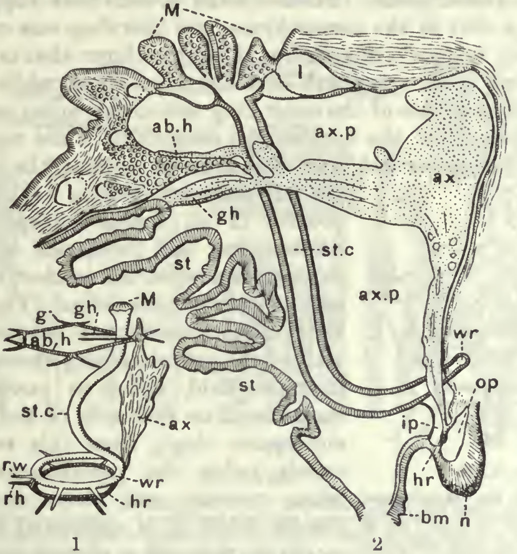


Fig. XXI.

Diagrams showing relations of pseudhaemal and water-vascular systems and axial organ in *Asterias rubens* (after Chadwick). 2 is × 50. *ab.h*, aboral haemal ring; *ax*, axial organ; *ax.p*, axial perihaemal canal; *bm*, buccal membrane; *g*, genital strands; *gh*, absorbent haemal strands leading from the gut-wall; *hr*, circumoral haemal ring; *ip*, inner perihaemal canal (cf. Fig. XXII.); *l*, blood lacunae; *M*, madreporite; *n*, nerve ring; *op*, outer perihaemal canal; *rw*, radial water-vessel; *rh*, radial haemal strands; *st*, stomach with folded wall; *st.c*, stone canal; *wr*, circumoral water-ring.

The sexes are nearly always separate, and fertilisation takes place in the water.

The Haemal Systems of Echinoderma are of two types, which may coexist, but of which one usually predominates. Neither is a true vascular system, but each consists of a series of smaller lacunae (spaces without definite walls) or larger sinuses, sometimes appearing as closed, but probably always having some communication, however minute or indirect, with the other cavities of the body. The fluid in these spaces differs from the ordinary coelomic fluid only in containing more albumen, and has, likewise, no definite circulation. The systems are: (*a*) **Pseudhaemal**, consisting of a ring placed between the ring and radial nerves of the oral system above, and the ring and canals of the water-system below. This system is dominant, perhaps the only one, in Stelleroidea, where it communicates with the general body-cavity and the axial sinus; it is present in Echinoidea and Holothurioidea, in which classes it is said to be closed; it is so much reduced in the Crinoidea that its existence is denied by some authors. In Asteroidea (Figs. XXI., XXII.) the ring is divided into an outer and an inner ring by an oblique septum, from each angle of which a vertical septum passes down each radial canal. Formerly the system was supposed to develop as a cleft in the mesenchyme, and therefore was called the "schizocoelic system"; MacBride (1896) has shown that in *Asterina* the inner ring is an outgrowth from the axial sinus, while each of the five compartments of the outer ring and canals arises separately as an outgrowth of the coelom, the outgrowth in the madreporic interradius being derived from the anterior coelom, the rest from the left posterior coelom. (*b*) **Lacunar**, present in all classes except perhaps Stelleroidea, and developed as lacunae or small spaces in the connective tissue, and therefore mesodermal (Fig. XXI.). It is differentiated into a network in the wall of the gut, absorbing therefrom the nutrient fluid, which is carried by a main trunk on each side of the gut to a circumoral ring; from this run radial canals, below the pseudhaemal canals when present, and above the water-vessels, while it is connected with networks on the surface of both gonads and axial organ. The lacunar system of the Stelleroidea differs in the absence of an absorbent network, and is, says Cuénot, a derivative of the axial organ, and therefore endodermal, *i.e.* it is only the pseudhaemal system greatly extended.

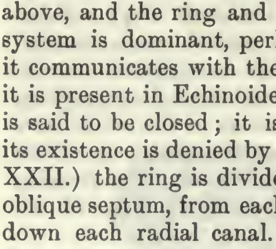


FIG. XXII.

Diagram of the pseudhaemal system of *Asterina* (after MacBride). Seen from above: *M* marks the M plane; *in* and *ex*, inner and outer divisions of the perihaemal ring; *a*, the one arising from the anterior coelom; *ax*, axial sinus, passing towards, but not opening into, the aboral perihaemal ring; *r.hc*, right hydrocoele; *g*, genital strands.

Respiration takes place through all exposed processes of the ambulacral system, and through the body wall where thin enough, as in some Holothurians. Specialised outgrowths or foldings of the latter are: the "external gills" of Echinoidea, outgrowths of the circumoesophageal sinus; the *papulae* of Asteroids, containing diverticula of the body cavity; the *bursae* of Ophiuroids; the "pectinirhombs" of some Cystids; the "hydrospires" of Blastoids and some Crinoids. Respiration is also effected by water entering the alimentary canal, whether through mouth or anus; in the latter case it is again expelled. Special structures connected herewith are: the "respiratory trees," which occur in some Holothurians as outgrowths from the cloaca; the anal tube of Crinoids, which in some Palaeozoic forms was large and with folded walls, forming the so-called "ventral sac"; the "accessory intestine" of Echinoids, a kind of by-pass, permitting water to flow through without interfering with the digestive process going on in the main gut.

Lymph-glands.—The amoebocytes are formed in specialised glandular regions of both haemal and ambulacral systems. Of the former nature are the radial and pharyngeal vesicles of Regular Echinoids, first described by Prouho (1888); the greater part of the Stelleroid lacunar system, just mentioned; and the "spongy organ" of Crinoids in the oral ring. Connected with the ambulacral system are the "Polian vesicles" found in most Echinoderms other than Crinoids, and the "Tiedemann's bodies" of Asteroidea (p. 243).

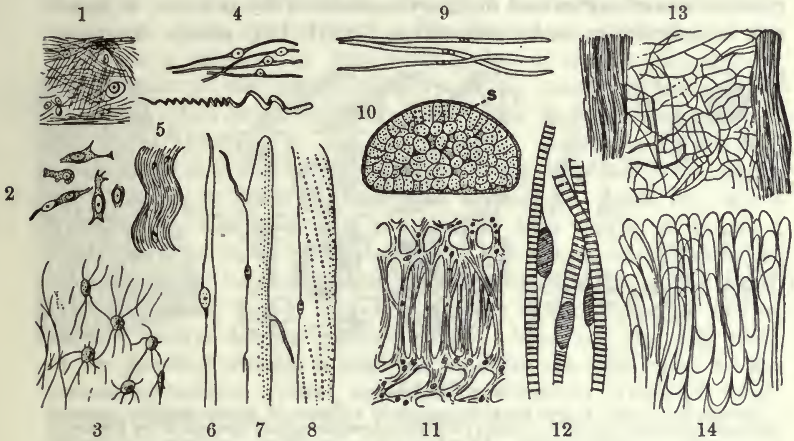


Fig. XXIII.

Echinoderm histology. 1, fundamental fibrous substance, with nuclei and an embryonic cell, from *Echinaster sepositus*. 2, stellate embryonic mesenchyme cells of *Asterias glacialis*. 3, gelatinous connective tissue of *Spatangus purpureus* (× 200). 4, elastic fibres of connective tissue from *Asterias glacialis*. 5, fibres from stalk of a pedicellaria of same. 6, muscle-fibre of same. 7, muscle-fibre from a spine attachment of *Toxopneustes lividus* (× 200). 8, muscle-fibre from jaw pyramid of same (× 250). 9, muscle-fibres from gut of *Sphaerechinus esculentus* (× 175). 10, transverse section through a muscle-bundle of *Asthenosoma urens*; *s*, sheath of connective tissue from which proceed septa that limit the smaller divisions. 11, stroma continued as fibrils across a suture in *Spatangus purpureus*, the stereom of the ossicles dissolved away. 12, transversely striate muscle-fibres of *Echinus acutus*. 13, dorsal ligament of arm of *Antedon* (× 125). 14, interarticular substance of *Isocrinus asteria*. 1, 2, 4, 5, 6 (after Cuénot). 3, 7, 8, 9 (after Hoffmann). 10 (after P. and F. Sarasin). 11, 12 (after Hamann). 13 (after W. B. Carpenter). 14 (after Joh. Müller).

The primitive **Mesenchyme** cells, derived chiefly by migration from the endoderm, partly from the ectoderm, have a large nucleus and indistinct, often amoeboid, cytoplasm. From them are developed connective and muscular fibres, amoebocytes and calcigenous cells, and intercellular, gelatinous, and fibrous substances. The **muscle-fibre** (Fig. XXIII. 6-9) derived from a single cell is smooth and straight, clearly defined at the ends, with a lateral nucleus. A few striated muscle-fibres are known in Echinoidea (Geddes and Beddard, 1881; Hamann, 1887). A semi-muscular, hyaline tissue of wavy, nucleated fibrils is peculiar to Crinoidea, and is called "ligament tissue." There are also muscles of endothelial origin. **Connective tissue** fibrils are nucleate and vary in length and shape; there are also rounded or stellate cells (Fig. XXIII. 4, 2). **Intercellular substance,** secreted by mesenchyme cells, often attains great thickness in the integument; it may remain a soft jelly, or become tough as indiarubber, or may split up into interlacing fibrils; it usually contains amoebocytes and ordinary connective tissue cells; it forms also interarticular substance (Fig. XXIII. 14), elastic ligament, and the walls of internal organs. Parallel structures are found in the cartilage of Vertebrata.

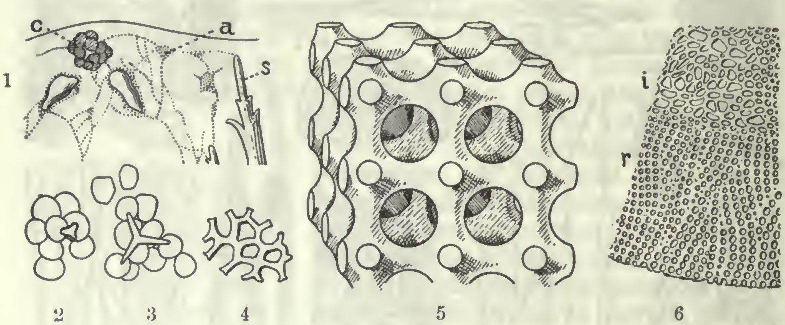


FIG. XXIV.

Stereom formation. 1, from the hinder portion of a *Pluteus* of *Echinus miliaris*. *s*, one of the large supporting rods of the *Pluteus*; *c*, a three-pronged spicule surrounded by a group of calcigenous cells, which derive their lime through a meshwork of pseudopodia and cells (*a*), from the rods of the *Pluteus* and from their broken ends, which are seen just below *c*. 2, 3, earliest stages of a spicule of *Echinocyamus*, surrounded by calcigenous cells. 4, infrabasal of an *Antedon* larva forty-eight hours old (× 230). 5, regular stereom from the outer part of the cup of *Holopus* (× 56). 6, portion of horizontal section of *Holopus* cup, showing relation of irregular (*i*) and regular (*r*) stereom (× 15). 1-3 (after Théel). 4 (after Seeliger). 5, 6 (after P. H. Carpenter).

The formation of a **calcareous skeleton** by the mesoderm was as pronounced in the oldest known Echinoderms as it is to-day, indeed, more so. To the prickly skin, so commonly a result of this, is due the name of the phylum (ἐχῖνος, a hedgehog; δέρμα, skin). Amoeboid cells in the mesenchyme have the power of fusing by pseudopodia into plasmodia or into reticular tissue (Fig. XXIV.). Where the pseudopodia meet and fuse, the protoplasm secretes a small calcareous spicule (intracellular, Théel; extracellular, Semon), which gradually increases in size along the lines of the pseudopodia. Such spicules meet and fuse by their processes, thus building up a hard tissue ("stereom"), with a structure that in section appears reticular, but really is more like a beam-and-rafter-work. As, in the growing Echinoderm, the protoplasmic reticulum becomes a more definite stroma, so the pattern of the stereom acquires definiteness, and varies in the different parts of an individual, as well as in different species. In the course of ages the spicules of the adult have themselves come to acquire definite shapes characteristic of species, and this is notably the case with the complicated "wheels," "anchors," and "tables" of Holothurians (Figs. II. 3, 6; V. 6, 7, pp. 222, 233); but, as Stewart and Bell have shown, also applies to the spicules of the thecal cavity in sea-urchins. The spicules of the theca usually fuse into plates, those of the appendages (brachia, stem, etc.) into ossicles. There is no real distinction; but it is often the case that the reticulum of the ossicles runs in straighter lines, while that of the plates is a more open mesh-work; this is due to the definite arrangement of the connecting fibres of the stroma in the appendages, and when this is definite in the theca the result, as we shall see under Cystidea (p. 42), is the same. Attempts to use this as an important character in distinguishing brachials from radials (p. 112), or a dorso-central from columnals, have no secure foundation. The stereom is absorbed by cells similar in outward appearance to those which deposit it, and the calcareous salts are transmitted by communicating pseudopodia from the absorbent to fresh depositing cells. Thus the spicules of the Echinoid *Pluteus* form a reserve for the growing urchin; thus, too, the anal plate of the growing *Antedon* is absorbed, and its material used by the increasing radials. Théel, to whose observations (1892-96) much of this knowledge is due, compares the reticular tissue, the osteoblasts, the osteoclasts, and the "Howship's foveolae" formed by the latter, of Vertebrata with the similar structures in Echinoderma. Bone in its first stages, especially that formed in connective tissue, is marvellously like Echinoderm stereom, and is likewise of mesodermic origin. But, whereas bone is an extracellular formation, it is probable that the spicules of Echinoderms, like those of Sponges, are intracellular. The otoliths of some Holothurians and the biscuit spicules of others (see p. 224) are distinctly intracellular formations. Bone, moreover, is phosphate, not carbonate, of lime, and does not retain the markedly crystalline character always possessed by Echinoderm stereom, even when highly complicated. Each skeletal element of an Echinoderm acts as a crystallographic individual, polarising light and cleaving along the planes characteristic of calcite. In fossils the cleavage is often emphasised by an infilling of the spaces with secondary calcite which has axes identical with those of the original crystal. According to Semon (1887), every skeletal element begins as a tetrahedron, usually in the form of a trifid spine with branches at an angle of 120°. The formation of similar spicules in sponges has been studied by Minchin (1898, see Part II., Chapter on Porifera).

The epiblast develops into an **ectoderm**, ciliated in whole or part. In the adult this often becomes merged in the mesoderm so as to be indistinguishable; in Ophiuroids it is for the most part calcified by the immigration of calcigenous cells; in Asteroids and Echinoids it remains with its cilia; in Crinoids it remains on the tegmen of some forms, and in the ventral grooves, where it is ciliated; in Holothurioidea it is very variable, being best preserved in Synaptidae. From the epithelium is derived the superficial "oral nervous system," composed of the circumoral ring and radial nerves. In Asteroidea and Crinoidea this remains on the surface, but in the other classes it sinks below, while the grooves in which the nerves originally lay are closed over them, forming "epineural canals" (Fig. XIII.).

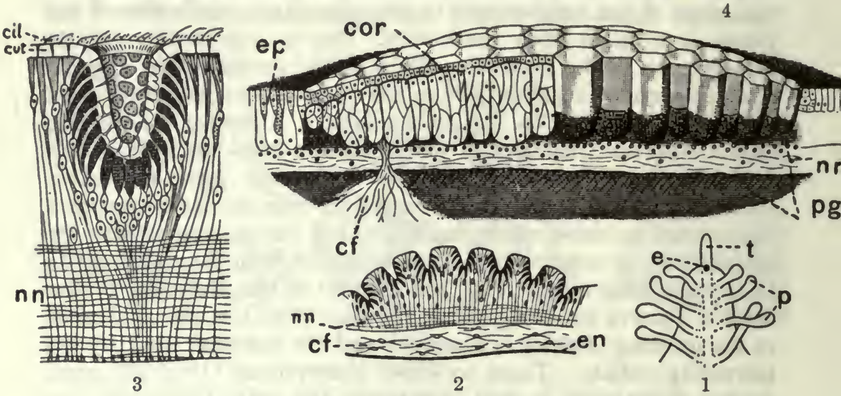


FIG. XXV.

Eyes of Echinoderms. 1, the end of a ray in young Asteroid. *t*, terminal tentacle; *p*, podia; *e*, eye-spot. 2, section across the eye-spot in *Asterias*, showing seven eye-cups. *en*, endothelium of perradial water-vessel; *cf*, connective tissue fibres; *nn*, nerve below epithelium. 3, section across an eye-cup (after Cuénot). *cil*, cilia; *cut*, transparent cutis, below which are the pigmented and retinal cells. 4, diagram of eye-spot of *Diadema setosum*, modified from Sarasin. The eye-spot, with its hexagonal elements, is surrounded by the pigmented integument, composed of a glandular, columnar epithelium (*ep*) which merges into the cornea (*cor*) above, and the eye-cups below; each cup is coated at its base with pigment (*pg*), and rests on a nervous layer (*nn*), below which is again pigment. Connective tissue fibrils (*cf*) pass through this in places.

Two other nervous systems are formed in Echinoderma: (*a*) the "deeper oral nervous system" from the mesoderm, underlying and roughly following the course of the superficial system; said to be absent in Crinoids, but is probably represented by their "sub-epithelial system"; present in all other Echinoderms except those Echinoids that have no masticatory apparatus; it chiefly innervates the muscles in the oral side of the body wall; (*b*) the "apical nervous system," most pronounced in Crinoids, and derived from the endothelium of the axial sinus; it is believed to occur in all other classes except Holothurioidea; it innervates the dorsal musculature of the test and appendages.

Sense-organs are but slightly developed. They are tactile, visual, and auditory or orienting. Tactile organs are furnished by the ambulacral appendages, the spines, and the pedicellariae. The chief among the ambulacral appendages is the "terminal tentacle," the unpaired end of the perradial water-canal, differentiated only in Stelleroidea and Echinoidea (Fig. XXV. 1). In Asteroids it is coated with columnar epithelium bearing long cilia and innervated by the radial nerve; in Ophiuroids this nerve, which is sub-epithelial in the arm, becomes epithelial in the tentacle; in Echinoidea the terminal tentacle is a sensory papilla penetrating the pore in the "radial" or "ocular" plate of the apical system. The remaining ambulacral appendages, the podia, whether sucking feet, as in Echinoidea, Holothurians, and Asteroids, or tentacles, as in Ophiuroids and Crinoids, are highly sensitive, and sometimes have special developments. Thus, on the adoral side of the oral tentacles of Synaptidae are two rows of papillae, of which the tip is concave and ciliated; these are called "sensory buds," and supposed to be organs of smell or taste. Again, the podia of Crinoids have small papillose projections, each papilla armed with three stiff but fine hairs. Similar papillae, sometimes more developed, occur in some Ophiuroids and Echinoids. Spines occur chiefly in Echinoids, less pronounced in Stelleroids, and rarely in Crinoids and Blastoids. Not all spines are sensory. The smaller spines of Cidaroida, surrounding the larger spines and the main openings of the theca, are covered with ciliated epithelium, and bear tactile hairs at the tip; the minute spines (*clavulae*) on the fascioles of Spatangidae (see p. 319) likewise have a ciliated integument, probably with sensory cells. The club-shaped spines of some Ophiuroids are covered with a glandular and sensory epithelium. *Pedicellariae* occur in all Echinoids, some Asteroids, and a few Ophiuroids; they are small, forceps-like appendages derived from spines (see p. 287). All are covered with a glandular, sensory epithelium, which in the "glandular pedicellariae" of some Echinoids develops special tactile prominences. Visual organs are known only in all Asteroids, a few Echinoids, and *Synapta*, but other (probably all) Echinoderms are sensitive to light, owing, perhaps, to the action of the pigment-bearing amoebocytes.

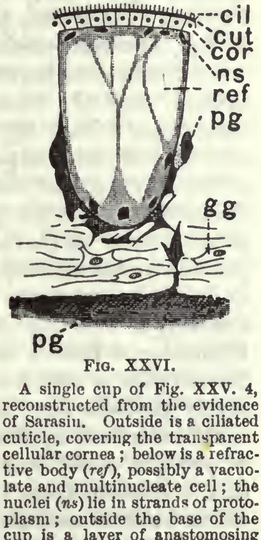


Fig. XXVI.

A single cup of Fig. XXV. 4, reconstructed from the evidence of Sarasin. Outside is a ciliated cuticle, covering the transparent cellular cornea; below is a refractive body (*ref*), possibly a vacuolate and multinucleate cell; the nuclei (*ns*) lie in strands of protoplasm; outside the base of the cup is a layer of anastomosing pigment cells, which pass up from the pigment layer below through the ganglionated (*gg*) nervous layer.

In Asteroids (Fig. XXV. 1) an eye-spot (*e*) lies at the base of each terminal tentacle (*t*) on its aboral side. This spot is a red cushion in which are many conical cups, each representing an eye (Fig. XXV. 2). The wall of each cup is formed of pigment cells and interspersed unpigmented retinal cells (Fig. XXV. 3). The Echinoid *Diadema setosum* has a black integument with numerous spots which, owing to interference of light, appear blue. Each blue spot, as proved by P. and F. Sarasin (1887), is a compound eye (Fig. XXV. 4). The structure of a single element is shown in Fig. XXVI. Supposed auditory organs ("Baur's vesicles" or otocysts) have been described only in some Holothurians, e.g. *Synapta* (see Fig. XVII. *oc*; also p. 234 and Fig. V. 5 on p. 233). The *sphaeridia* of Echinoids (see p. 288) are supposed to be organs of orientation, or of taste and smell (Lovén), or for appreciating chemical changes in the water (Ayers, 1885). They occur only on the oral side of the theca, and when the animal is in the natural position they hang down like the clapper of a bell; but when the animal is tilted, each sphaeridium presses against the nerve cushion surrounding its stalk.

Distinctive Characters of Phylum and Classes.—The foregoing account has introduced the fundamental features of Echinoderm morphology, laying stress on characters common to the whole Phylum rather than on those that distinguish the various classes. It has, however, tended to show the inner meaning of those outward distinctions between the chief types with which the chapter opened, and the student may perhaps have realised that "the homologies within the Echinoderm stock" are, as Semon has insisted, often more apparent than real. In drawing up a definition of the Phylum that shall include the most primitive forms of fixed Echinoderms known, one cannot utilise most of the characters usually thus employed in systematic treatises, since they are secondary, homoplastic acquisitions, often with no true homology. It is, for instance, not sure that all Echinoderms have a radiate symmetry, even an obscured one. It is true that all recent Echinoderms have a lacunar, haemal system; but that system in Stelleroidea is not homologous with the one in Crinoidea. It is highly probable that all animals to which the name "Echinoderm" could have been applicable since the beginning have had a portion or portions of the anterior coelom specialised as a hydrocoel; but this is different from the questionable assertion that all Echinoderms have an ambulacral system.

On the other hand, in any attempt to limit the several classes, respect should be paid to deep-seated structures illustrative of past history and genetic affinity rather than to the obvious but superficial differentiations that characterise the representatives now living. We have to make our classificatory partitions run back as far as possible. Since the factor determining the lines of evolution appears to have been position with regard to the sea-floor, this must no longer be contemned as "mere difference of habit." The first Echinoderms were not necessarily fixed, but fixation probably affected all representatives of the Phylum at an early period and produced gradual changes, the first being the migration of the mouth and left hydrocoel to the upper pole. Those forms in which the oral pole remained uppermost, whether actual fixation by the aboral pole persisted or no, are to be distinguished from those in which the oral pole again shifted, accompanied by loss of fixation. Leuckart's term Pelmatozoa (1848), though primarily connoting the actual or potential possession of a stalk, has come into general use for the former group. The term Statozoa, proposed by Bell (1891), implies absence of locomotion, and is therefore not so great an improvement as to compel its adoption. The term Crinoidea was extended by Roemer (1851) to include all Pelmatozoa, but such extension does violence to the intentions of J. S. Miller, the coiner of the name (1821). The forms with oral pole uppermost may, it is true, be divided into classes; but, as maintained by Huxley and Ray Lankester, their genetic connection is so evident that it should be recognised by the establishment of a Sub-phylum, to which we shall continue to apply the name Pelmatozoa. The included classes, as hereafter explained, are the Cystidea, Blastoidea, Crinoidea, and Edrioasteroidea. The remaining classes of Echinoderma have been placed together by P. H. Carpenter and others as Echinozoa, but may more conveniently be spoken of as Eleutherozoa (a term originally used by Bell in a sense excluding Holothurians). Their genetic connection, however, is only that due to descent from the Pelmatozoa; even if all Eleutherozoa descended from one class of Pelmatozoa, they did so at widely differing periods. The Holothurians must have cast loose before the genital organs had been affected by radial symmetry, and are thus, as well as by the horizontal position of the oro-anal axis and the retention of the *M* plane as sagittal, sharply distinguished from Echinoidea and Stelleroidea. The two classes last mentioned were with some reason opposed by Leuckart to Pelmatozoa and Holothurioidea (or Scytodermata, as he called the latter) as Actinozoa; but they differ in important features. If Cuénot's interpretation of the lacunar systems be correct, it seems as though the Echinoidea branched off before radial symmetry had greatly affected the coelomic lacunar system derived from the axial sinus; similarly the digestive system retained its coiled and non-radiate arrangement; moreover, the sinking of the ambulacral water-vessels and nerves below the test here diverged further from the Pelmatozoic type than is the case in Asteroidea. The extension of the ambulacra nearly to the aboral pole in Echinoidea and the development of a special terminal plate at the end of each ray in Stelleroidea afford features of much diagnostic value, but of less morphological importance. English writers have usually regarded the Asteroidea and Ophiuroidea as well-defined classes. The normal forms are in fact markedly separate, but the evidence of ontogeny, as well as the existence of connecting links now, and the approximation of the two groups in Palaeozoic time, renders this view difficult of acceptance, so that they are here combined in a class Stelleroidea.

Diagnosis of Echinoderma.—Metazoa, coelomata, triptoblastica, living in salt or brackish water, with a primitive bilateral symmetry still manifest in the right and left divisions of the anterior and posterior coelom; with a hydrocoel primitively developed from each half of the anterior coelom, and connected with the exterior by a water-pore; with stereom composed of crystalline carbonate of lime deposited by special amoebocytes in the meshes of a mesodermal reticulum or stroma, chiefly in the integument (absent only in the highly modified *Pelagothuria*, p. 230, and, according to Koehler, in the Holothurians *Stichopus pallens* and *S. torvus*); with gonads derived from the endothelium, apparently of the anterior coelom; total segmentation of the ovum produces a coeloblastula and gastrula by invagination; mesenchyme is formed in the segmentation cavity by migration of cells, chiefly from the hypoblast.

Known Echinoderma show the following features (imagined to be due to an ancestral Pelmatozoic stage):—Increase in the coelomic cavities of the left side and atrophy of those on the right; the dextral coil of the gut, recognisable in all classes, though often greatly obscured; an incomplete secondary bilateralism about the plane including the main axis and the water-pore or its successor, the madreporite, often obscured by one or other of various tertiary bilateralisms; the development of the hydrocoel into a circumoral, arcuate or ring canal, the hydrocircus; except in the small (but increasing) number of known cases in which care of the brood has secondarily arisen, development is through a free-swimming, bilaterally symmetrical, ciliated larva, of which in many cases only a portion is transformed into the adult Echinoderm.

All living, and most extinct, Echinoderms show the following features (almost certainly due to an ancestral Pelmatozoic stage): —An incomplete radial symmetry, of which five is usually the dominant number, is superimposed on the secondary bilateralism, owing to the outgrowth from the peristome of one unpaired and two paired ciliated grooves; these have a floor of nervous epithelium, and are accompanied by subjacent radial canals from the hydrocircus, giving off lateral podia and thus forming ambulacra, and by a pseudhaemal system of canals apparently growing out from coelomic cavities.

All living Echinoderms have a lacunar, haemal system of diverse origin. This, the ambulacral system, and the coelomic cavities contain a fluid holding albumen in solution and carrying numerous amoebocytes, which are developed in special lymph-glands and are capable of wandering through all tissues.

The Echinoderma may be divided into seven **Classes**, the mutual relations of which are roughly represented in the annexed table.

Pelmatozoa { Cystidea ——— Edrioasteroidea
|
Blastoidea
|
Crinoidea }

— Holothurioidea
— Echinoidea
— Stelleroidea } (Eleutherozoa)

Guide to Literature of Echinoderma Generally.

In selecting from the large mass of writings, preference has been given to the more recent, especially those giving summaries or bibliographies. Works alluded to in the text may also be found by reference to the *Zoological Record* and the *Zoologischen Jahresberichten* (Naples).

1. *Agassiz, A.* 1882. (Echinodermata . . . Bibliography.) Bull. Mus. Comp. Zool. Harvard, vol. x. pp. 109-134.
2. —— 1883. (Selections from Embryological Monographs—II. Echinodermata.) Mem. Mus. Comp. Zool. Harvard, vol. ix. (2), pp. 1-45, pls. i.-xv.
3. *Bell, F. J.* 1891. (On the Arrangement and Interrelations of the Classes of the Echinodermata.) Ann. Mag. Nat. Hist., ser. 6, vol. viii. pp. 206-215.
4. *Buetschli, O.* 1892. (Versuch der Ableitung des Echinoderms aus einer bilateralen Urform.) Zeitsch. wiss. Zool., vol. liii. Suppl. pp. 136-159, pl. ix.
5. *Bury, H.* 1888. (The Early Stages in the Development of *Antedon rosacea.*) Phil. Trans. Roy. Soc. London, vol. clxxix. (1888), B., pp. 257-300, pls. xlii.-xlvii.
6. —— 1889. (Studies in the Embryology of the Echinoderms.) Quart. Journ. Micr. Sci., N.S. vol. xxix. pp. 409-449, pls. xxxvii.-xxxix.
7. —— 1895. (The Metamorphosis of Echinoderms.) Quart. Journ. Micr. Sci., N.S. vol. xxxviii. pp. 45-135, pls. iii.-ix.
8. *Carpenter, P. H.* 1878-85, -87. (Notes on Echinoderm Morphology—i.) Quart. Journ. Micr. Sci., N.S. vol. xviii. pp. 351-383 ; (ii.) vol. xix. pp. 176-206 ; (iii.) vol. xx. pp. 321-329 ; (iv.) vol. xxi. pp. 169-193, pls. xi., xii. ; (v.) vol. xxii. pp. 371-386 ; (vi.) vol. xxiii. pp. 597-616 ; (vii.) vol. xxiv. pp. 1-23, pl. i. ; (viii.) vol. xxiv. pp. 319-327 ; (ix.) vol. xxv. Suppl. pp. 139-155 ; (x.) vol. xxvii. pp. 379-391 ; (xi.) vol. xxviii. pp. 303-317.
9. *Crety, C.* 1894. (Contribuzione alla conoscenza dell' ovo ovarico.) Ric. Lab. Anat. Roma, vol. iv. pp. 261-281, pl. xiv. [Contains Bibliography.]
10. *Cuénot, L.* 1891. (Études morphologiques sur les Echinodermes.) Arch. Biol., vol. xi. (1891), pp. 313-680, pls. xxiv.-xxxi. [Gives good Bibliography.]

11. *Durham, H. E.* 1891. (On Wandering Cells in Echinoderms, etc., more especially with regard to Excretory Functions.) Quart. Journ. Micr. Sci., N.S. vol. xxxiii. pp. 81-121, pl. i.

12. *Field, G. W.* 1892. (The Larva of *Asterias vulgaris.*) Quart. Journ. Micr. Sci., N.S. vol. xxxiv. pp. 105-128, pls. xiii.-xv.

13. —— 1895. (On the Morphology and Physiology of the Echinoderm Spermatozoön.) Journ. Morph., vol. xi. pp. 235-270, pls. xv.-xvi.

14. *Foettinger, A.* 1880. (Sur l'existence de l'hémoglobine chez les Échinodermes.) Arch. Biol., vol. i. pp. 405-413, pl. xvii.

15. *Geddes, P.* 1880. (Observations sur le fluide périviscéral des oursins.) Arch. Zool. Exper., vol. viii. pp. 483-496, pls. xxxvii.-xxxviii.

16. —— *and Beddard, F. E.* 1882. (On the Histology of the Pedicellariae and the Muscles of *Echinus sphaera*, Forbes.) Trans. Roy. Soc. Edinb., vol. xxx. pp. 383-395, pls. xix.-xxi.

17. *Hamann, O.* 1883-89. (Beiträge zur Histologie der Echinodermen, Heft 1.) Zeitschr. wiss. Zool., vol. xxxix. pp. 145-190 and 309-333, pls. x.-xii. and xx.-xxii. (Heft 2), pp. iv. and 126, pls. i.-vii., 8vo, Jena, 1885. (Heft 3), Jena. Zeitschr., vol. xxi. pp. 87-266, pls. vi.-xviii. (Heft 4), Jena. Zeitschr., vol. xxiii. pp. 233-388, pls. xii.-xxiii.

18. *Howell, W. H.* 1886. (Note on the Presence of Haemoglobin in the Echinoderms.) Stud. Biol. Lab. Johns Hopkins, vol. iii. pp. 289-291, pl. xviii.

19. *Lang, A.* 1896. Text-book of Comparative Anatomy, translated by H. M. and M. Bernard, Part II. pp. 284-560, 8vo, London. [Contains a good classified Bibliography.]

20. *Leuckart, C. G. F. R.* 1848. Ueber die Morphologie und die Verwandtschaftsverhältnisse der wirbellosen Thiere, etc., 8vo, pp. viii. and 180, Braunschweig.

21. *Ludwig, H.* 1880. (Ueber den primären Steinkanal der Crinoiden nebst vergl.-anatom. Bemerkungen ueber die Echinodermen ueberhaupt.) Zeitschr. wiss. Zool., vol. xxxiv. pp. 310-332, pls. xii., xiii.

22. *MacBride, E. W.* 1896. (The Development of *Asterina gibbosa.*) Quart. Journ. Micr. Soc., N.S. xxxviii. pp. 339-411, pls. xviii.-xxix.

23. *MacMunn, C. A.* 1885. (On the Chromatology of the Blood of some Invertebrates.) Quart. Journ. Micr. Sci., N.S. vol. xxv. pp. 469-490, pls. xxxiii., xxxiv.

24. *Metschnikoff, E.* 1869. (Studien über die Entwickelung der Echinodermen und Nemertinen.) Mem. Acad. Sci. St. Petersb., ser. 7, vol. xiv. No. 8, 73 pp. 12 pls.

25. —— 1885. (Ueber die Bildung der Wanderzellen bei Asterien und Echiniden.) Zeitschr. wiss. Zool., vol. xlii. pp. 656-673, pls. xxv.-xxvi.

25*a*. *Mortensen, T.* 1898. (Die Echinodermen-larven der Plankton-Expedition nebst einer systematischen Revision der bisher bekannten Echinodermenlarven.) Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, vol. ii. part J, 120 pp., 9 pls., and 1 map. Also published in Danish, as doctoral thesis, 1897; and in Vidensk. Meddel. for 1898. [Gives a good Bibliography.]

26. *Müller, Joh.* 1848. (Ueber die Larven und die Metamorphose der Ophiuren und Seeigel.) Abh. k. Akad. Wiss. Berlin, Phys. Kl. 1846, pp. 273-312. 7 pls.

27. —— 1849. (Ueb. L. und M. d. Echinodermen), *op. cit.* 1848, pp. 75-109, 5 pls.

28. *Müller, Joh.* 1850. (Ueb. L. und M. d. Holothurien und Asterien), *op. cit.* 1849, pp. 35-72, 7 pls.

29. —— 1852. (Ueb. L. und M. d. Echinodermen), *op. cit.* 1850, pp. 37-86, 9 pls.

30. —— 1852. (Ueber die Ophiurenlarven des Adriatischen Meeres), *op. cit.* 1851, pp. 33-62, 8 pls.

31. —— 1853. (Ueber den allgemeinen Plan in der Entwickelung der Echinodermen), *op. cit.* 1852, pp. 25-65, 8 pls.

32. —— 1854. (Ueber den Bau der Echinodermen), *op. cit.* 1853, pp. 123-219, 9 pls.

33. —— 1855. (Ueber die Gattungen der Seeigellarven), *op. cit.* 1854, pp. 1-55, 9 pls.

34. *Sarasin, P. B. and C. F.* 1887. (Die Augen und das Integument der Diadematiden.) Ergebnisse naturw. Forsch. auf Ceylon, Bd. I. Heft 1, 4to, Wiesbaden.

35. —— 1888. (Ueber die Anatomie der Echinothuriden und die Phylogenie der Echinodermen), *tom. cit.* Heft 3.

36. *Seeliger, O.* 1893. (Studien zur Entwicklungsgeschichte der Crinoiden. *Antedon rosacea.*) Zool. Jahrb., Abth. f. Morph., vol. vi. pp. 161-444, pls. xii.-xx. [Gives Bibliography of *Antedon* embryology.]

37. *Semon, R.* 1888. (Die Entwickelung der *Synapta digitata* und die Stammesgeschichte der Echinodermen.) Jena. Zeitschr., vol. xxii., N.F. xv., pp. 175-309, pls. vi.-xii.

38. —— 1889. (Die Homologien innerhalb des Echinodermenstammes.) Morph. Jahrb., vol. xv. (2), pp. 253-307.

39. *Sladen, W. P.* 1884. (On the Homologies of the Primary Larval Plates in the test of Brachiate Echinoderms.) Quart. Journ. Micro. Sci., N.S. vol. xxiv. pp. 24-42, pl. i.

40. *Théel, H.* 1892. (On the Development of *Echinocyamus pusillus* [O. F. Müller]). Nova Acta R. Soc. Sci. Upsala, Ser. III. pp. 1-57, pls. i.-ix. [Summarises previous writings.]

41. —— 1894. (Notes on the Formation and Absorption of the Skeleton in the Echinoderms.) Svensk. Vet. Akad. Förhandl., 1894 (8), pp. 345-354.

42. —— 1896. (Remarks on the Activity of Amoeboid Cells in the Echinoderms.) Festskrift för Lilljeborg, pp. 49-58, pl. iii., Upsala.

See also Nos. 27, 64, 95, 96, in Literature of Pelmatozoa (p. 211); Nos. 25, 32, 41, in Literature of Stelleroidea (p. 279); and Nos. 36, 39, 62, in Literature of Echinoidea (p. 328).

CHAPTER IX.

THE PELMATOZOA—CYSTIDEA.[1]

GRADE A. PELMATOZOA, LEUCKART (1848)
(= CRINOIDEA, *sensu lato Auctt.*).

CLASS I. CYSTIDEA.
„ II. BLASTOIDEA.
„ III. CRINOIDEA.
„ IV. EDRIOASTEROIDEA.

ECHINODERMA with the viscera enclosed in a calcified and plated theca, of which the oral surface is uppermost, and which is usually attached, either temporarily or permanently, by the aboral surface. Food brought to the mouth by a subvective system of ciliated grooves, radiating from the mouth either between the plates of the theca (endothecal), or over the theca (epithecal), or along processes from the theca (exothecal: arms, pinnules, etc.), or, in part, and as a secondary development, below the theca (hypothecal). Anus usually in the upper or oral half of the theca, and never aboral. An aborally placed motor nerve-centre gives off branches to the stroma connecting the various plates of the theca and of its brachial, anal, and columnar extensions, and thus co-ordinates the movements of the whole skeleton. The circumoesophageal water-ring communicates indirectly with the exterior; the podia, when present, are respiratory, not locomotor, in function.

The origin and meaning of many of these characters have already been discussed in the general section. The origin of others will be traced in following the history of the Grade; and many of them will be more fully discussed under Crinoidea, in which class alone are they adequately known.

The classes of Pelmatozoa here adopted are of very unequal value; and to place them either in a line or side by side does not represent their phylogenetic relations. Such, probably, would be better shown by placing a primitive class, Amphoridea, at the base and deducing from it several lines of descent, viz. Edrioasteroidea, Anomalocystida, Aporita, Rhombifera, and Diploporita. From the Edrioasteroid line, we may suppose, there sprang first Holothurians, then Stelleroidea, then Echinoidea, while the line itself still survived in more specialised forms to the close of the Carboniferous period. The Diploporite line ought properly to include the Blastoidea; and from it probably there arose, as a fresh development with a new lease of life, the important class, Crinoidea. The other lines were unsuccessful and none survived the Silurian. But to make the classification coincide absolutely with this history, which after all is not yet proven, would be to reject names and classes that have held the field for more than half a century in favour of new and unaccepted terms. Old names, therefore, have been retained so far as possible. The diversity of existing opinion, however, may serve as excuse for a few novelties. Such are the use of Haeckel's Amphoridea, in an emended sense; the resuscitation of Edrioasteroidea; the emendation of the Rhombifera, Aporita, and Diploporita, and of the included families, which, when not new, are rarely used in the sense of the original proposer; the extension of the Blastoidea, and their division into Proto- and Eu-blastoidea; a considerable revision of the accepted classification of Eublastoidea; and a recasting of the classification of Crinoidea.

---

[1] By F. A. Bather, M.A. Since the majority of Pelmatozoa, being of extinct types, present peculiar difficulties, the student unfamiliar with Echinoderm structure is recommended to begin either with the description of a simple Crinoid (Chapter XI.), or that of a Starfish (Chapter XIV.).

CLASS I. CYSTIDEA, Von Buch (1844).

Order 1. **Amphoridea.**
„ 2. **Rhombifera.**
„ 3. **Aporita.**
„ 4. **Diploporita.**

Pelmatozoa in which radial polymeric symmetry of the theca is developed either not at all or not in complete correlation with the radial symmetry of the ambulacra (such as obtains in Blastoidea and Crinoidea); in which extensions of the food-grooves are exothecal or epithecal or both combined, but neither endothecal nor pierced by podia (as in Edrioasteroidea).

The earlier and more primitive Cystidea represent the pelmatozoic stage through which the Echinoderm race passed, on its way from the Dipleurula to the various classes. They shed light not only on the origin of those classes, but on the still more ancient ancestor of the Phylum. The remarkable adaptability of the Echinoderm type, the mode of origin of many organs, and the biological phenomena of homoplasy and convergence, can also be studied in this class.

The Cystidea were first separated from other Echinoderms, under that name, by L. v. Buch in 1844 and 1845. His definition laid stress on the fixed condition, the irregularity of the thecal plates, and the absence of arms like those of Crinoidea. Subsequent discoveries of stemless cystids, of cystids with radial symmetry in the theca, and of arm-like structures in most cystids, have made the letter of this definition untenable; but its spirit holds good. The difficulty that this class has presented to systematists is chiefly due to these factors: (1) The rarity and ill-preservation of these old Palaeozoic fossils; (2) the ancestral nature of the group and the consequent existence of links between it and other groups; (3) the wrongful ascription to the Cystidea of various genera (e.g. *Porocrinus*, *Stephanocrinus*, *Hypocrinus*, *Echinocystis*); (4) the extraordinary diversity of structure in the class, a feature common to most groups at their origin, and productive in this case of many lines of development, only a few of which have become so severed from the rest as to be regarded as independent classes (*e.g.* Blastoidea and Crinoidea, distinguished by all; Edrioasteroidea, distinguished by a few; Anomalocystidae, not distinguished, but quite as separate); (5) the rapid development of the class, from the exceedingly simple *Aristocystis* to such highly specialised forms as *Lepadocrinus*, *Caryocrinus*, and *Mesocystis*. Hence the diagnosis cannot be elaborate, and must be mainly negative.

Most of the **classifications** hitherto proposed have been based upon one set of characters; thus Zittel's (1879) adaptation from Johannes Müller (1854) is according to the structure of the thecal plates (Aporitidae, Diploporitidae, Rhombiferi); Barrande's division (1887), not intended as taxonomic, is according to the number of openings in the theca. A far better arrangement is that initiated by Pictet (1857), extended by Bronn (1859), and modified by Dujardin and Hupé (1862); this, however, is rather a key to genera than a classification into orders and families. Attempts have also been made (*e.g.* Forbes, 1848; and Neumayr, 1889) to determine the lines leading from the Cystidea to other classes; and on such principles Steinmann (1888) founded his classification into Eucystoidea, Cystechinoidea, Cystasteroidea, and Cystocrinoidea. A classification on true phylogenetic principles was first published by Haeckel (1896), who only failed from want of acquaintance with the facts of Cystid structure. The classification in this text-book attempts to express the actual lines of descent as inferred from an independent study of the fossils.

The main lines of descent are these. The starting-point is a simple, many-plated, sac-like form (e.g. *Aristocystis*, Fig. II. p. 44), in which neither ciliated food-grooves, though perhaps present, nor radial ambulacral vessels, have left any trace on the skeleton, in which the porous structure of the stereom is indefinite, and in which no stem is differentiated. Modifications of this soon appeared in many directions. In one direction arose an antero-posterior flattening of the theca and the extension of food-grooves along two lateral articulated spines, with a peculiar and characteristic arrangement of stereom; this was accompanied by development of a stem (Anomalocystidae, pp. 49, 52, Figs. XI.-XIII.). In another direction was an extension of the theca downwards to form a stem, and upwards from the mouth to form a single jointed process for the support of a ciliated groove (Dendrocystidae, p. 47, Fig. IX.). Neither Anomalocystidae nor Dendrocystidae proceeded very far, and they may conveniently be grouped with Aristocystidae and a few other primitive forms into an order, AMPHORIDEA, distinguished from the rest chiefly by absence of radial symmetry in food-grooves and ambulacra.

A very different modification was that which produced a theca flattened horizontally, with five ciliated grooves passing from the mouth between its plates ("endothecal"), and protected by distinct covering-plates; ambulacral vessels lay beneath or within the grooves, and podia from them passed between the adjacent thecal plates. So different is this type from those of other Echinoderma, that such forms have here been separated as a class, EDRIOASTEROIDEA (Chapter XII.).

Returning to the primitive Amphoridea, we find a difficulty in distinguishing some of them from their immediate descendants, owing to the very slight traces left on the theca by the originating extensions of the food-grooves. Those forms in which such traces are perceptible may almost from the outset be grouped under two heads. One group includes those in which the grooves wander outwards from the mouth over the thecal plates, which gradually become arranged regularly on either side of the grooves, while still further extensions ascend from the "epithecal" grooves on small "exothecal" processes called "brachioles." In the other group the grooves do not tend so much to stretch over the theca as to be raised away from it on relatively larger brachioles, arising in the immediate neighbourhood of the mouth.

At the same time, a difference manifests itself in the structure of the thecal plates. From the indefinite relations of stereom and stroma noticed in earlier Amphoridea arise two types of structure (Fig. I.). The canals traversing the stereom, more or less perpendicularly to the thecal surface, either cease to be simple ("haplopores") and become connected in pairs ("diplopores") still perpendicular to the surface; or they come to lie parallel to the surface and at right angles to the sutures. In the latter case we may suppose that the canals represent stroma strands continuous across the sutures; those crossing any one suture come to occupy a rhombic area bisected by the suture-line, and, since, in weathered plates, there appear to be pores at the ends of these canals, the areas have been called "pore-rhombs" (*Poren-rauten*, see Fig. XV., *Echinosphaera*, and XVI., *Orocystis*). There also takes place a gradual increase in the area, and a decrease in the number, of the thecal plates relative to the size of the theca; perhaps the folds that often radiate from the umbo of each plate are connected with this, for they must have strengthened the plates, like the folds in corrugated iron or pasteboard. These folds may coexist with diplopores or with pore-rhombs; but they are clearly more adapted to the latter structure, and often seem to merge with it and accentuate

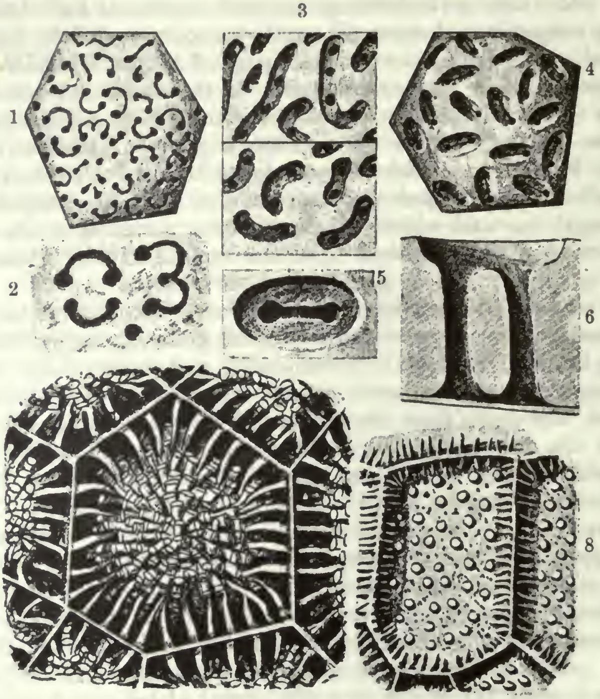


FIG. 1.

Structure of the test in Aristocystidae. 1, plate of *Aristocystis bohemicus* showing haplopores, some of which are connected by a horse-shoe canal, ×4; 2, portion of same further enlarged; 3, portions of surface of other specimens, gradually leading up to such a structure as in 4, a plate of *Calix Sedgwicki*, with diplopores; 5, a diplopore of rather different form; 6, section of a diplopore; the hypostereom is shown, but the epistereom, if there were any, is removed; 7, a natural replacement (by infiltration of mineral matter) of the original stroma-strands and sutures in plates of *Calix* (?), the stereom dissolved away; 8, plates of *Aristocystis* in similar condition showing vertical strands (=haplopores) in the middle, and radiating strands at the sutures. All figures enlarged. (1, 2, 3, and 8 after Barrande; 4 and 7 after Rouault.)

it. Thus is evolved a highly specialised type of stereom-folding known as a "pectini-rhomb." Now, although it is difficult to separate all the forms at the first parting of the ways, it is soon seen that diplopores are almost confined to the genera with epithecal extensions of the subvective system, while those with only exothecal extensions are characterised by pore-rhombs or pectini-rhombs. There is therefore justification for the old divisions DIPLOPORITA and RHOMBIFERA, as orders, in a restricted sense.

The Diploporita (p. 70) show a gradually increasing regularity of structure in the food-grooves, and in their relations to the theca, leading almost imperceptibly to the Blastoidea. So much is this the case that it seems well to separate from the Cystidea certain forms in which "the radial polymeric symmetry" *is* "in complete correlation with the radial symmetry of the ambulacra" (see definition, p. 39), and to refer them to the Blastoids as an order Protoblastoidea (p. 79). The only alternative is to make the Blastoids an order of the Cystidea.

In many of the Rhombifera (p. 52) a peculiar modification of the food-grooves takes place, in that they are continued over the theca, not directly on the thecal plates themselves, but by a proliferation of plates from the mouth region. The grooves thus formed have been termed "recumbent arms" or "pseudambulacra," and are fringed with brachioles. This type of ambulacral structure was independently developed in this order more than once; but it is most common in the group of genera characterised by pectini-rhombs and by pentamerism in the theca (family Glyptocystidae, p. 58). A group with pore-rhombs highly developed inside the theca, and with hexamerous symmetry, is distinguished as the family Caryocrinidae (p. 65). In it the food-grooves tend to be enclosed by thecal plates ("hypothecal").

The orders already mentioned do not include all genera that come under the terms of our definition of Cystidea. From early forms of Rhombiferi, or perhaps even directly from Amphoridea, there arose a small group in which neither diplopores nor pore-rhombs were developed, at all events to the same extent, but the number of thecal plates was greatly lessened and exothecal brachioles were developed. The best known of these is *Cryptocrinus* (p. 69). One might adopt APORITA (*sens. str.*) as an ordinal name.

ORDER 1. **Amphoridea**, Haeckel (1896, *pars*).

Primitive Cystidea in which radial symmetry has affected neither food-grooves, nor thecal plates, nor, probably, nerves, ambulacral vessels, nor gonads.

Haeckel included under this name rather more forms than are here referred to it, and separated them from the Cystidea as a primitive class of Echinoderma, comparable to the Pentactula stage passed through in the development of all their descendants. The more characteristic and undoubted Amphoridea, however, represent only a stage in the development of the Echinoderm type and not a divergence; they are too intimately connected with more specialised Cystidea to warrant separation as a class. It should also be remembered that, though such a stage as this probably was actually passed through, still forms are liable to be referred here, owing to our ignorance of their true structure.

Family 1. Aristocystidae. Amphoridea without extension of food-grooves, epithecally, endothecally, or on exothecal skeletal processes. Theca composed of numerous plates without regular arrangement or specialised structure. No stem. Genera—*Aristocystis*, Barrande (1887), Ordovician, Bohemia (Fig. II.), is in many respects the simplest Echinoderm known. The ovoid theca is composed of 150-200 plates, of no definite shape or arrangement, but with a tendency in the narrower, aboral half of the theca to form transverse rows of elongate hexagons. The animal usually fixed itself to some solid body by a portion of the theca at or near the lower pole (*B*). At the upper pole is the mouth (*O*), a wide slit in the transversal plane, with slightly raised edges. About a third of the way down the theca is the round anal opening (*As*), 6-8 mm. in diameter, closed by six or seven triangular plates, meeting in the centre, and known as "the valvular pyramid." Between mouth and anus, and usually a little to the left, are two smaller openings—a transverse slit (*M*) close to the mouth; and a round pore (*G*) close to the anus. Of these *M* is regarded by P. H. Carpenter (1891) as the hydropore, and *G* as the gonopore, a view accepted by Haeckel (1896) and adopted here. There is no trace of calcified arms or brachioles, whether jointed or solid, nor even of epithecal or hypothecal extensions from the hydrocoel ring or from the mouth. The *hydrophores palmées* described by Barrande, and supposed by Neumayr (1889) and P. H. Carpenter (1891) to be subtegminal ambulacra, are really epithecal food-grooves, and have not been proved to belong to this genus. The plates of the theca are thick, especially at its lower end; they are said by Barrande to be composed of three layers (Fig. III.): (*e*) outer, thin, smooth, and solid; (*m*) middle, thick, pierced by irregular canals, more or less at right angles to the outer surface; (*h*) inner, thin,

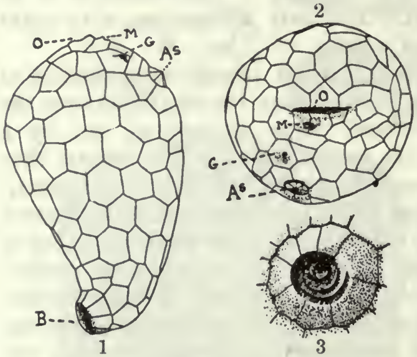


Fig. II.

Aristocystis bohemicus. 1, side view; 2, oral view, both ½ nat. size; 3, base, showing impression of Gastropod shell, ×⅔. The lettering is explained in the adjoining text. (All adapted from Barrande.)

passing up into the suture lines and into the ends of the canals, smooth on its inner surface. Doubt has been cast on the existence of these three layers, but examination of well-preserved specimens suggests the following interpretation:—(*m*) is homologous with the "mesostereom" of all Echinoderms, its plates were deposited in a stroma of connective tissue, and presented not only large meshes, but continuous larger canals for the passage of strands of stroma, and perhaps of lacunar blood-vessels: the stroma was thus continuous throughout each plate, and strands often passed over the outer surface, uniting the larger strands and sometimes producing the grooves bent in horse-shoe, as at 2 in Fig. I.; (*e*) is not a truly calcified epistereom, but probably represents a hard epidermis; there is little doubt that some structure did actually cover the outer ends of the canals; (*h*) represents the inner layer of the integument, which towards the margins of each plate was often differentiated into elastic or muscular strands, uniting adjacent plates and giving flexibility to the theca; if calcified, this layer would be homologous with the "hypostereom" of many Crinoids, but, as in the case of (*e*), there is only preserved to us the space which it occupied, filled with subsequent infiltration or with iron oxide precipitated during the decomposition of the organic matter. The primitive features of *Aristocystis* are then: indefinite shape of theca, indefinite arrangement of plates, undifferentiated

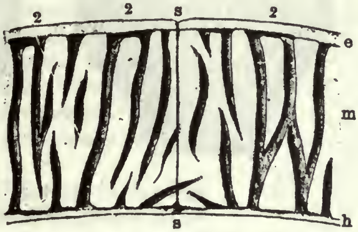


Fig. III.

Section of test in *Aristocystis*, in the region of a suture (*s*). Shows epistereom (*e*), mesostereom (*m*), and hypostereom (*h*). *m* is pierced by haplopores which are joined above at 2, 2. (Original diagram, magnified about 10 diam.)

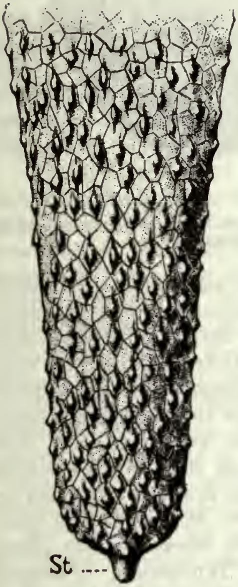


Fig. IV.

Calix Sedgwicki, from a reconstruction by Rouault; about nat. size.

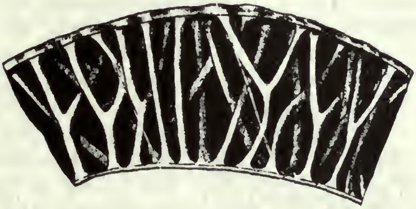


Fig. V.

A transverse section of a plate of *Calix Murchisoni*, the stroma-strands replaced by infilling matrix, the stereom dissolved away. × 6 diam. (After Rouault.)

structure of stereom, absence of stem and of definite base of attachment, absence of arms, absence of ambulacra, a single and independent gonopore as in Holothurians. *Calix*, Rouault (1851-78; syn. *Craterina*, Barr. pars, 1887), Ordovician, France and Bohemia (Fig. IV.). The theca is a bowl or vase of very thick plates, with an oral covering of very thin ones rarely preserved. There is usually a marked hollow at the lower end, but *C. Sedgwicki*, Rouault's type-species, has a short, stem-like prominence (*St*). The canals in the plates tend to definiteness of arrangement, especially at the lower end, where they seem to radiate from the hollow. The connection of the canals at their outer ends, to form pairs, is often marked (Fig. V.). All these characters are exaggerations of some already noted in *Aristocystis.* The tenuity of the upper surface, and its consequent disappearance in most specimens, have permitted the recognition of only one aperture, which is pentagonal, and probably represents the anal pyramid (Fig. VI. 2). Specimens with *hydrophores palmées* have been referred to this genus, but belong to (p. 73) Diploporita. *Pilocystis*, *Lapillocystis*, and *Acanthocystis*, Cambrian, and *Baculocystis*, Ordovician, Bohemia, all described by Barrande, are probably referable to this order if not to this family. *Lodanella*, Kayser (1885), Lowest Devonian, Germany, though called a sponge, is very like *Calix*. *Deutocystis*, Barr. (1887), Ordovician, Bohemia (Fig. VII.), is distinguished from *Aristocystis* by the greater irregularity in size of the thecal plates (comparable to the arrangement of plates in the carapace of some extinct edentates, Glyptodontidae), and by the absence of an independent gonopore, this having fused either with the anus or with the hydropore. There are signs of fixation by the aboral end of the theca (*B*), where the plates are larger and tend to lie in rows. The

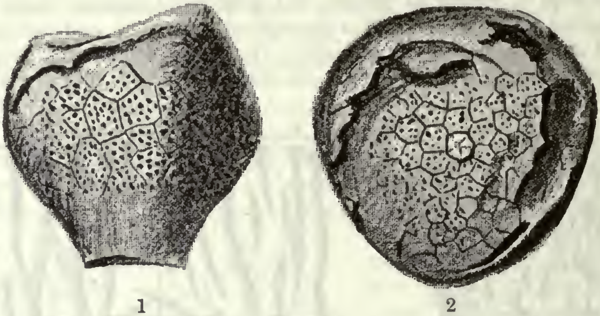


Fig. VI.

1, *Calix bohemica*, from the side; towards the base the pores are covered by a smooth epidermis. 2, *C. excavata*, the tegmen. Both nat. size. (After Barrande.)

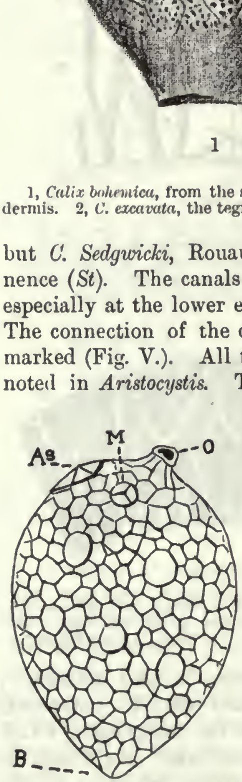


Fig. VII.

Deutocystis modestus, restored on the evidence of Barrande, pl. 15, II. 3. Lettering as in Fig. II.

mouth (*O*) is surrounded by five large plates, forming a slight projection, somewhat eccentric. The anal pyramid (*As*) has five plates. The hydropore (*M*), a little to the right of the line joining mouth and anus, was covered by a small pyramid of three plates, the impressions of which on the internal cast (the only part preserved) have been regarded as three openings. The canals in the thecal plates are more numerous near their margins. Certain species, in which the plates seem more rounded, not closely apposed, and perhaps without canals, in which the anal pyramid had four plates, and in which the hydropore was not tripartite (*i.e.* had no valvular plates), have been separated by Haeckel (1896) as a genus, *Amphoracystis*. *Pirocystis*, Barrande (1887), Ordovician, Bohemia (Fig. VIII.), had a pear-shaped theca truncate below for fixation (*St*), but still without true stem. The anal pyramid had six plates (*As*); otherwise it was much like *Deutocystis*. The regularity of the adoral plates in these two genera suggests that they may eventually prove to be early forms of Diploporita or Rhombifera.

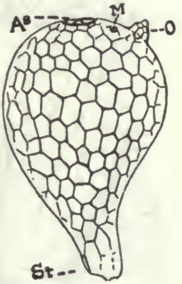


Fig. VIII.

Pirocystis pirum, restored outline on the evidence of Barrande, pl. 29. Lettering as in Fig. II.

The Lower Niagara rocks (Silurian) of Indiana and neighbouring states have yielded numerous forms resembling *Aristocystis* in external appearance and structure of theca, but with an ambulacral system apparently presenting three grades of organisation. They have all been described under the generic name *Holocystites* or *Holocystis*, a name previously given to a coral, and therefore bound to yield to the alternative *Megacystis*, Hall (1864-65). Some of the so-called species described by Hall and S. A. Miller seem to agree with *Aristocystis* in the entire absence of arms and food-grooves, in the similar position and structure of mouth ("ambulacral orifice," S. A. M.), and anus ("mouth," S. A. M.), while a hydropore ("anus," S. A. M.) is often observable, and occasionally a fourth opening (? gonopore); the positions of the two latter are at varying distances between mouth and anus. Miller has described other species with similar structure, but with four or five of the plates surrounding the mouth raised into elliptical facets, apparently for the support of spines like those of *Placocystis* (p. 51); no groove connects these facets with the mouth, although in some species the mouth assumes a tetragonal or pentagonal outline, with angles directed towards these facets. The third and higher stage of organisation, possibly developed from this one, is seen in *Holocystites gyrinus*, Miller and Gurley (1894), and must be referred to the Sphaeronidae (see p. 72).

Family 2. Dendrocystidae. Amphoridea with a single oral skeletal process, theca composed of numerous irregular plates, extending below gradually into a stem. The single genus, *Dendrocystis*, Barrande (1887), Ordovician, Bohemia and Russia (Fig. IX.), has a theca in shape and intimate structure not far removed from that of Aristocystidae; of equal thinness all over, its plates irregularly polygonal, and their strands of mesostroma not so well-defined. The following differences are of great importance:—The theca suddenly thins below to about one-third its width, forming a tubular extension (*St*), the walls of which contain numerous small plates, which gradually become larger and more definite in arrangement, and merge into a tube with a narrow lumen enclosed by comparatively large solid plates. Comparison with more highly developed genera shows that this extension is a stem (*columna*), and its presence indicates a more fixed habit than was, perhaps, assumed by Aristocystidae. Further influence of fixation is clear in the development at the opposite pole of the theca of a movable, jointed tube (*Br*), composed of four or five rows of small plates, wider than high, and often alternating; this tube tapers to a rounded end, in which no opening is perceptible; neither are there openings between its plates; the plates may, however, have opened along one of the vertical lines, thus converting the tube into a groove, exactly as figured in Fig. 5 of Barrande's Plate XXVI. (see Fig. IX.). This organ was regarded by Barrande and Trautschold as a *tubus ventralis* for genital (not faecal) products; by Neumayr (1889) as an arm, with a double row of ambulacral pores; by Haeckel (1896) as an oral proboscis, or possibly the stem. It is here regarded as an extension from the mouth, bearing a ciliated food-groove that could be closed by plates, and perhaps also an extension from the water-ring. Other thecal openings are doubtful; an anal pyramid may have existed in the lower third of the theca (*As*), but Barrande's figures and descriptions are inconsistent; hydropore and gonopore quite unknown. Folds or ridges radiate from the centre to the edges of each thecal plate; besides strengthening the plates, these folds, like similar ones in later stalked forms, may indicate the concentration of a nervous layer in the integument into definite tracts (axial nerves) putting the stem, thecal plates, and plates of food-grooves into connection. *Cigara*, Barrande (1887), resembles the stem of *Dendrocystis*, and suggests its occurrence in the Cambrian. *Syringocrinus paradoxus*, E. Billings (1859), is the same thing from Quebec.

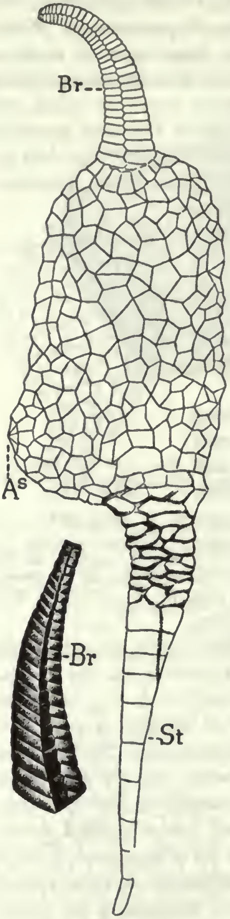


Fig. IX.

Dendrocystis Sedgwicki, restored on the evidence of Barrande. *Br*, the arm-like appendage, copied from Barrande.

Family 3. Eocystidae. Established to include certain obscure forms from the Lower and Middle Cambrian of Great Britain and North America. *Eocystis*, Billings (1868), and *Protocystis*, Hicks (1872, see also Salter, 1873), have never been properly described or figured; but since they cannot well be distinguished from *Eocystites* (?) *longidactylus*, Walcott (1886), that species must be taken as the example of the family (Fig. X.). Thecal plates numerous, irregular, "varying in form, size, and surface characters on the same body." The two important points are: the varying development of radiating stereom-folds on some of the plates; the presence around the mouth of not less than ten biserial brachioles, with long covering-plates ("short pinnulae," Walcott). This type, therefore, is intermediate between Amphoridea and Rhombifera, and its occurrence at so low a horizon is fortunate for the phylogenist. This family Eocystidae in no way corresponds to Haeckel's Eocystida, which, like his *Eocystis*, is a purely imaginary creation of no systematic validity.

FAMILY 4. ANOMALOCYSTIDAE. Theca compressed in the plane of the thecal apertures, one side tending to be convex, the other concave. Plates of the two sides enclosed by a common frame of marginals. Plates of concave side tend to be fewer and more regular than those of convex, but never achieve bilateral symmetry as do the latter. Tapering stem of polymeric columnals at one end of theca; at the opposite end are the apertures, with function still uncertain. In some genera, spines ("arms" of most writers) are known, one at each upper angle of the theca. Ornament of granules, which on the theca tend to run in transverse, wavy, sub-parallel lines, simulating the scale-markings of some Crustacea. No pores. J. Walther (1886) and Haeckel (1896) have considered the bilateral symmetry primitive, and homologous with the Dipleurula; but M. Neumayr (1889) maintained that the symmetry of the two was different. The evidence suggests that the evolution was *towards* greater

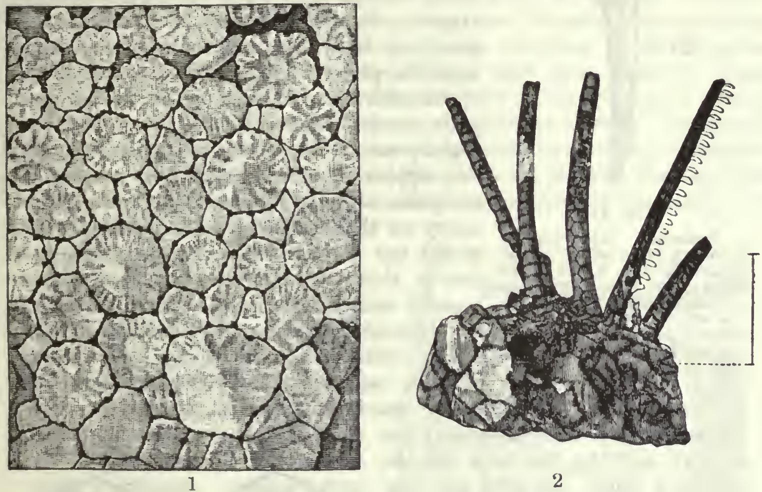


FIG. X.

Eocystis longidactylus. 1, portion of test much enlarged, showing variation in size, outline, and markings of plates, some of which have apparent pores at their edges; 2, upper part of a specimen without test, showing portions of brachioles and impressions of covering-plates. With kind permission of Dr. C. D. Walcott.

bilateral symmetry, and therefore started *from* the usual sack-like form. Genera—*Trochocystis*, Barrande (1859-87 ; syn. *Trigonocystis*, Haeckel), Cambrian, Bohemia, France, Spain (Fig. XI.), is the most primitive ; its theca is bounded by twelve stout marginals (*mm*), conspicuous on one side more than on the other, and forming a circular, elliptical, or subtriangular frame ; the enclosed space on either side is occupied by a mosaic of 80-160 somatic plates, hexagonal except where truncated by the marginals. At the oral end of the frame three openings, nearly in the broad median plane, pass from the thecal cavity through or between the marginals to the exterior; the middle opening (? hydropore and gonopore) is widest, and is protected by a hood-like projecting plate (*M*), (? madreporite) ; of the other two openings, one (*O*) in the broad plane is the wider (? mouth), the other (*As*) slightly out of that plane is smaller (? anus) ; they appear to be connected by a canal (? for reception of gut) running round the thecal cavity on the inside of the marginals. At the aboral end of the frame the marginals pass into a short, tapering stem (*St*) of subtriangular section, composed of rows (3 or 5 ?) of alternating ossicles, its lumen communicating with the thecal cavity. *Trochocystis* may be regarded as a differentiation from such a form as *Aristocystis* by lateral compression, so that its broad median plane is morphologically the sagittal, and the flat sides are the primitive right and left, the projecting plate *M* being on the left side. *Mitrocystis*, Barrande (1887), Cambrian and Ordovician (Fig. XII.), has twelve marginals (*mm*), but on the (left ?) side that corresponds with the convex side of later forms, the junction of the stem with the somatic plates lies between two of them ; while the median adoral plate of this side (*M*) is vertically grooved on the interior, but exteriorly resembles the somatic plates, which on this side, though larger and fewer (50-60) than in *Trochocystis*, still form a mosaic of hexagons ; two, adjoining the stem, are larger than the others. On the other side, which corresponds with the concave side of later forms,

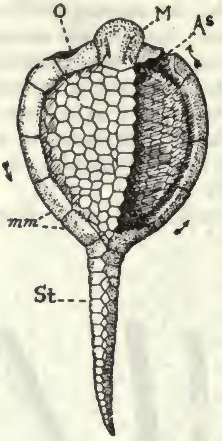


Fig. XI.

Trochocystis bohemicus, restored on the evidence of Barrande's figures. A part of the theca on the right of the figure is removed showing the interior. The arrows show the supposed direction of the gut. The letters are explained in the adjoining text.

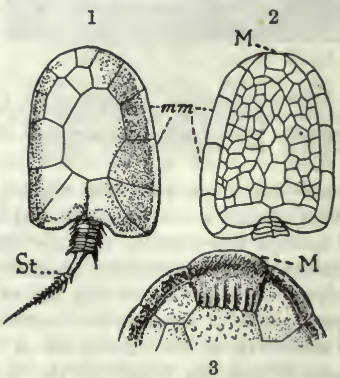


Fig. XII.

Mitrocystis mitra. 1, from supposed right side ; 2, from supposed left side ; 3, interior of upper part of the latter, showing the folded plate *M*. (After Barrande.)

the marginals have extended far over the area formerly occupied by somatic plates, and these latter number from three to six, one of which is much the largest and of irregular shape. Openings other than the median not distinct. Stem of about four alternating rows of plates, often provided with thorn-like processes, and each overlapping its distal neighbour; total length about equal to that of the theca, the proximal third with a wide lumen. No other appendages observed. *Atelecystis* (*A. Huxleyi*), Billings (1858), is imperfectly known; *Anomalocystis cornutus*, Hall (1859), may be congeneric, as usually supposed; but *A. disparilis*, Hall, probably belongs to *Placocystis* (*vide infra*). All the species described by Barrande (1887) as *Anomalocystis* are doubtful. The specimens described by Meek (1873) and Wetherby (1879) are separable generically under the latter's name, *Enoploura;* the species are *E. balanoides*, Meek sp., and *E. crustacea*, Haeckel sp.[1] In all these one traces the gradual diminution in number of plates, especially of somatic plates, and the evolution of the granular ornament into wavy ridges. Some of these also show traces of adoral spines. *Belemnocystis* is placed in this family by Miller and Gurley (1894), probably with justice, though its exact affinities are obscure. *Platycystis*, S. A. Miller (1889), is based on a worn Anomalocystid of indeterminable affinities. *Placocystis*, de Koninck (1869), from the English Wenlock beds of Silurian age (Fig. XIII.), is the most specialised form of this family. It was redescribed by H. Woodward (1880); since then fresh knowledge has been gained. On either side of the concave face (Fig. XIII. 1) are three marginals (*mm*) which pass over on to the convex side; at the columnal end are two marginals, at the oral end are three, and none of these five continue on to the convex side, although corresponding plates occur there. The median adoral marginal of the convex side (Fig. XIII. 2) is the plate M; its free edge is occasionally denticulate (cf. ridgings in *Mitrocystis*). The somatic plates of the concave side are one large central, and one small at its left upper corner: those of the convex side are eleven, viz. two ad-columnal, as in *Mitrocystis*, supporting one median which does not touch the column as it does in *Enoploura;* a transverse row of five, the median of which is small and often quite surrounded by its two neighbours (it is *not* an anal structure, as supposed); a row of three adjoining the adoral marginals. Stem much as in *Mitrocystis.* The three marginals that meet at each adoral angle of the theca (Fig. XIII. 3) form an articular surface (*Br'*) for the support of a spine

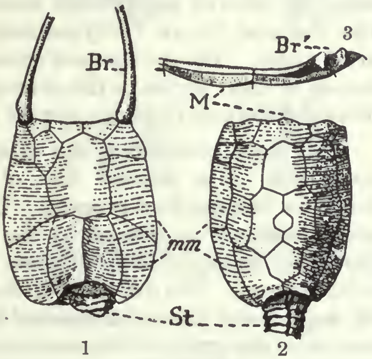


Fig. XIII.

Placocystis Forbesianus. 1, concave or supposed right side; 2, convex or supposed left side; 3, upper margin, showing attachment for spine at *Br'*. (1, reconstructed from various specimens in British Museum; 2, from Brit. Mus., E7545, enlarged; 3, from the type-specimen, Brit. Mus., E7588.)

---

[1] This name must be restricted to Wetherby's Fig. 1, *d, e, f,* and ?*g*.

(*Br*) which may attain 2/3 the length of the theca, without signs of a joint. The spine is subcircular in section, and has no groove and no accessory plates ; none the less it may have served as an arm, *i.e.* as the bearer of a tentaculate extension of the water-system, and of a ciliated path to the mouth. The mouth, anus, and hydropore were probably situated in the integument uniting the two sides of the thecal opening that seems to stretch between the spines. Haeckel (1896) supposes that the *Apus*-form of the Anomalocystidae was correlated with locomotion, and that the stem was a locomotor organ—a suggestion by no means far-fetched ; but his statement that the anus was ad-columnal must have been based on *Pleurocystis* (p. 64), which, though belonging to a different order, simulates *Placocystis* in many features.

ORDER 2. **Rhombifera**, Zittel (1879, emend.)

Cystidea in which radial symmetry affects the food-grooves, and, in the more advanced families, the thecal plates ; probably also the nerves and ambulacral vessels, but not the gonads. The food-grooves are exothecal, *i.e.* are stretched out from the theca on jointed skeletal processes (brachioles). These either are close to the mouth or are removed from it upon a series of ambulacral or subambulacral plates not derived immediately from thecal plates, or are separated from the oral centre by hypothecal passages passing beneath tegminal plates. The stereom and stroma become arranged in folds and strands at right angles to the sutures of the thecal plates ; in higher forms the stereom-folds are in part specialised as pectini-rhombs.

The chief reason for the establishment of this order is the recognition of a distinct line of development in the skeletal structures bearing food-grooves. That this represents a true phylogenetic series is confirmed by the structure of the test, although there may be some indefiniteness in this respect shown by the earlier genera. The difficulty of classifying forms at the parting of the ways is not one to be lessened by advance of knowledge. We note also the gradual decrease in number of thecal plates, their increasing subjection to a radial symmetry, and greater development of a stem. Hence, as is to be expected in a natural classification, there is a far greater difference apparent between extremes in the same series, say, the Callocystinae and the Echinosphaeridae, than between the latter and the Diploporite family Sphaeronidae, which constitute initial forms of different series. The radial symmetry or actinism of the order is trimerous, pentamerous, or hexamerous, but may undergo secondary modification through atrophy of a ray (e.g. *Comarocystis, Lepadocrinus*).

FAMILY 1. ECHINOSPHAERIDAE. Rhombifera in which the thecal plates are numerous and indefinitely arranged. So-called pore-rhombs are developed, but no pectini-rhombs. Brachioles confined to neighbourhood of mouth, unbranched. Stem, when present, not composed of a single series of columnals. This family includes some of the Cystidea earliest studied. *Echinosphaera* and *Sphaeronis* (p. 71) are found in the rocks around the Baltic as round balls filled with radiating crystals of calcite. Hence they were known to the older Scandinavian naturalists as "crystal apples," and were, as such, included by Linnaeus in his Mineral Kingdom, under the name *Aetites.* Their animal nature was first demonstrated by the youthful Gyllenhal (1772) in an admirable paper. He further recognised, not merely their echinoderm affinities, but also that essential difference between the tests of the two forms which was emphasised by Joh. Müller eighty-two years later, served as the basis of Zittel's classification, and is still regarded as an ordinal character. So little were these forms understood that König (1825) placed *Echinosphaera aurantium* near the Ascidian, *Boltenia*, under the name *Leucophthalmus Strangwaysi;* while in 1845 M'Coy compared a *Sphaeronis* to the Ascidian, *Chelyosoma.* These comparisons, though based on superficial similarity, without bearing on the supposed relationship between Echinoderma and Enteropneusta, have again been brought forward by Haeckel (1896). Genera—*Echinosphaera*, Wahlenberg (1818 ; synn. *Crystallocystis, Citrocystis, Trinemacystis*, Haeckel), Ordovician, Europe, type *Echinus aurantium*, Gyll. (Fig. XIV.). The smooth, spheroidal theca is composed of some hundreds of irregular plates, mostly hexagonal. At the aboral pole the plates, arranged in one or two fairly regular circlets, form a slight projection (*St*), by which probably the theca was attached, but there was no definite stem. At the oral pole is another projection (*O*), very variable in size and shape ; this, as shown by Volborth (1846), supports arms. From the figures published by Volborth (1846), Müller (1854), Quenstedt (1876), Angelin (1878), and Haeckel (1896), it appears that the plates forming the oral projection, as well as the arms themselves, vary in number and position (Fig. XV.). The primitive number of arms appears to be three, one anterior, *i.e.* opposite the anus, and two lateral. The two lateral may fork, thus producing five branches in all

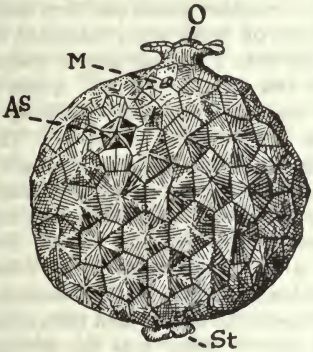


FIG. XIV.

Echinosphaera aurantium, after Volborth. The lettering is explained in the adjoining text. Nat. size.

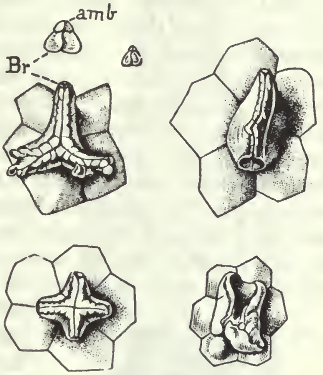


FIG. XV.

Peristomial areas of *Echinosphaera aurantium*, showing variation in origin of brachioles (*Br*). (After Volborth.) Enlarged.

(cf. p. 11). In either of these cases the anterior arm may diminish in size and finally disappear, leaving either two lateral, or two antero-lateral + two postero-lateral = four branches in all. The length of the arms and their subsequent branching, if any, are unknown. The portions preserved are formed of series of brachials, bearing on their adoral (upper) surfaces a groove leading to the central mouth, and roofed by small covering-plates. The anus (*As*), with its pyramid of four to ten plates, lies 1/3 or 1/4 of the way down the theca. Between anus and mouth, to the right, is the hydropore (*M*). The plates of the theca were united by strands of mesostroma as in the next genus. *Arachnocystis*, Neumayr (1889), of Ordovician age, has for type the *Echinosphaerites infaustus* of Barrande (1887). The pear-shaped theca is composed of 200-800 plates of irregular shape and arrangement, mostly small, but with a few larger plates interspersed. At the narrower end of the theca is a stem, about 40 mm. long, composed of five (?) alternating rows of hexagonal plates. At the opposite pole lies the mouth, on a slight elevation of larger, irregular plates (*not* five orals as sometimes stated). From these are given off three arms, composed of two alternating rows of plates (biserial), and with a ventral groove roofed by small covering-plates ; they may reach 100 mm. in length. About a third of the way down the theca is the large anal opening, closed by a pyramid of five plates. The hydropore has not been observed. The structure of the thecal plates is clearly shown in the Bohemian fossils ; between the thin non-porous epistereom and hypostereom lies the mesostereom, penetrated by canals left by the strands of mesostroma that ran at right angles across the sutures and united the plates. A trace of the original path of these strands, as seen in *Aristocystis*, remains in the form of canals passing down to the hypostereom, one at the ad-central end of each transverse canal, and one on either side the suture. The centre of each plate is solid, and often raised in an umbo ; by ideal lines drawn from the umbo to the angles of each plate, the canals are grouped in triangles, and the adjacent triangles of two neighbouring plates form a "pore-rhomb." *Palaeocystis*, Billings (1858), Ordovician, Canada, has thecal plates of similar structure. *Orocystis*, Barrande (1887), Ordovician, Bohemia (Fig. XVI.), has an oviform theca, with a small hexagonal stem (*St*) of unknown length, and near the other pole three eccentric openings : *O* generally, and probably with right, regarded as the mouth ; *As* the anus ; *M* the hydropore. The thecal plates are marked with strong axial folds, parallel with which are smaller ridges, all at right angles to the sutures. The folds are probably the superficial indications of axial nerves, and it is noteworthy that strongly marked folds radiate from the six angles of the stem, and that six

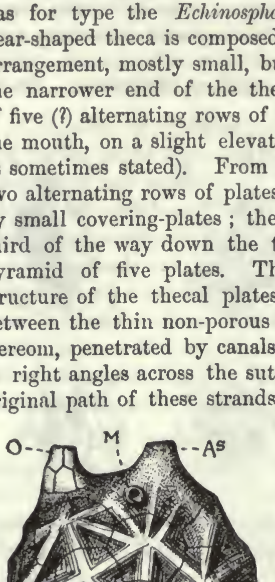


FIG. XVI.

Orocystis Helmhackeri, restored on the evidence of Barrande's figures and descriptions.

similar folds lead to the oral aperture (possibly conveying nerves to six brachioles). The minor ridges are the superficial indications of strands of mesostroma, uniting plate to plate across the sutures, and emerging on the inner surface in rows of apparent pores. *Heliocrinus*, Eichw. (1840; syn. *Heliocystis*, Haeck.), Ordovician, Europe, has for type *Echinosphaerites balticus*, and therefore includes numerous species of similar structure, usually referred to *Caryocystis.* It differs from *Echinosphaera* in the more pronouncedly pentagonal, though minute stem, and in the greater ornamentation of the cup by axial folds and ridges. *Stichocystis*, Jaekel (1899), has apparent pores in the ridges. *Caryocystis* was founded by von Buch (1844 and 1845) to receive *Echinosphaera granatum*, Wahlenberg (*Sphaeronites testudinarius*, Hisinger, *non Auctt.*), and another species which von Buch and all subsequent authors have incorrectly supposed to be *S. testudinarius*, Hisinger. Eichwald (1859), aware that *C. granatum* belonged to his own *Heliocrinus*, justly took as the type the second species mentioned by von Buch, adding to it *C. pumila*, an Echinoencrinid. The type of the genus is therefore the species universally and erroneously known as *C. testudinarius*, which name yields to *C. Angelini*, Haeckel (Fig. XVII.). *Amorphocystis*, Jaekel in Koken (1896), is a simple synonym. *Caryocystis* differs from *Heliocrinus* in the elongation of the oral and aboral poles, and the elongation of the mouth in the sagittal plane. At each end of the mouth-slit, Angelin's figure (1878; our Fig. XVII.) shows two facets for brachioles (*Br′*); it also seems to show two openings (hydropore, *M*, and gonopore ?, *G*) between mouth and anus.

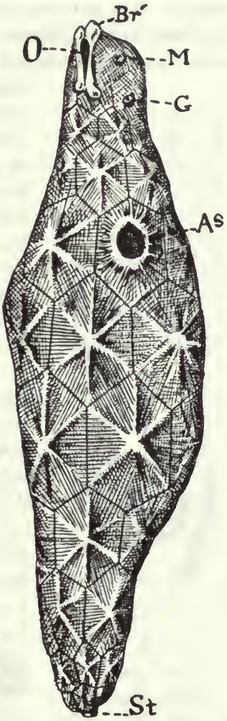


Fig. XVII.

Caryocystis Angelini (*C. testudinarius*, Auctt.). (After Angelin.) × $\frac{3}{2}$.

Family 2. Comarocystidae. Rhombifera in which thecal plates are numerous and indefinitely arranged. Radial structure of stereom strongly marked, but no definite pore-rhombs or pectinirhombs. Food-grooves on free exothecal brachioliferous processes. Columnals in a single series. Genera—*Comarocystis*, Billings (1854), Ordovician, Canada. Theca ovate, may be over 7 cm. high, composed of about 150 mostly hexagonal plates, with strongly marked radial striation of the stereom, especially towards the margins, which are raised above the umbones of the plates. Mouth-slit transverse, with a pair of uniserial brachioliferous arms at either end. Theca flattened in mouth-plane. Anus below arms on right side. Hydropore above level of anus, near the posterior margin of the mouth. Stem longer than theca; columnals low, circular, with moderately wide lumen. *Achradocystis*, Volborth (1870), Ordovician, Russia, appears to have an anal pyramid of seven plates, and a very highly developed stem. Thecal plates have strong radiating ridges, marginal concentric ridges, and suture margins toothed on the inside in correspondence with the ridges. Since this structure is not unlike that in *Comarocystis*, the genus is provisionally placed here.

FAMILY 3. MACROCYSTELLIDAE. Rhombifera in which the theca consists of three or four circlets of plates, subjected to a more or less regular pentamerism. The stereom is strongly radiately ridged or folded, but no so-called "pores" or pectinirhombs are developed. Brachioles are borne by the upper circlet of plates, and within these there may have been tegminal plates over the mouth. There is perhaps no intimate connection between the two genera referred to this family. But they are both Cambrian, and show an early development of that tendency to reduce the number of plates, which eventually evolved the Glyptocystidae from a different branch of the Rhombiferi. The Macrocystellidae were probably derived from Eocystidae without passing through an Echinosphaerid stage. Genera—*Macrocystella*, Callaway (1877), Upper Cambrian, Shropshire. Theca seen from the side (Fig. XVIII. 1) shows four circlets of plates, apparently five in each circlet. Those of the aboral circlet are low and pentagonal; those of the second and third circlets hexagonal and relatively large; those of the fourth circlet about half the size of those in the third, sub-pentagonal, and each bears a brachiole. These almost immediately bifurcate, making ten branches in all, about as long as the theca is high, and apparently biserial; covering-plates are distinct. There were probably tegminal plates above the origins of the brachioles. Thecal plates strongly marked with radiating folds, which divide the surface into triangles; between them are smaller folds. No fine rhomb structure is seen. Anus unknown. Stem rapidly tapering, about half as long again as total length of crown; proximal columnals low and imbricating, with very wide lumen; distal columnals long and narrow. *Mimocystis*, Barr. (1887), Ordovician, Bohemia, does not, so far as can be gathered from the published description, differ from *Macrocystella* in any essential. *Lichenoides*, Barr. (1846, 1887; Pompeckj, 1896; syn. *Lichenocystis*, Haeckel), Cambrian, Bohemia and Bavaria. Theca composed of rounded plates of very different sizes, but semi-regular in arrangement. At the base are five to twelve minute plates, indicating absence of stem and probably of fixation, at all events in adult. Above those is a circlet of five irregularly pentagonal large plates. Resting on, and to a certain extent alternating with these, are six or seven plates of similar size. A circlet of smaller plates, alternating with the last mentioned, forms the summit, and bears about eight biserial unbranched brachioles. No anus observed.

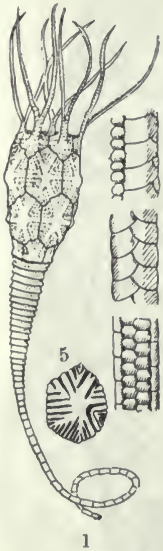


FIG. XVIII.

Macrocystella Mariae. 1, from side (reconstructed from Brit. Mus., E7523 and E7524), × $\frac{1}{3}$; 2-4, portion of a brachiole, × 8, from side, dorsal, and ventral surfaces; 5, single plate of a large specimen (Brit. Mus., E7528), nat. size.

All plates except the minute ones at the base were united by strong stroma-strands across their sutures, and these form pore-rhombs.

FAMILY 4. TIARACRINIDAE. Rhombifera in which the plates forming the sides of the theca are arranged in not more than two circlets, and the plates of each circlet are transversely united by strongly marked pore-rhombs. The genera, though clearly separated as offshoots from the Rhombifera, do not form a very coherent group, and need careful description by a well-informed worker. *Tiaracrinus*, Schultze (1867, Syn. *Staurosoma*, Barrande, 1887), Devonian, Eifel, and Bohemia. Theca cup-shaped or a truncate spheroid, the sides composed of four large, interradially situated plates, one of which is (? only in some cases) horizontally bisected. These plates are united by strongly marked stereom-folds, raised above the surface, and forming demi-rhombs. The composition of the oral surface is unknown, but there seems to have been a central mouth, with food-grooves radiating from it towards the margin, where brachioles probably arose. An anus seems to have pierced the margin at the summit of one of the triangular side-plates. Stem-facet four-sided, with angles radial; lumen small. *Rhombifera*, Barrande (1867 and 1887), Ordovician, Bohemia. Theca elongate, triangular in section; appears composed of two circlets—a lower, of three plates united by strong stereom-folds, visible exteriorly only as terminal pores outlining "pore-rhombs"; an upper, of six (?) plates, of which three pairs are united by pore-rhombs, similar to those of the lower circlet, and vertically above, not alternating with them. Oral region unknown. Aboral region passes gradually, by smaller plates, into a cylindrical stem. The structure of the pore-rhombs and the trimerous symmetry suggest comparison with Caryocrinidae. *Rhombifera mira*, Barr., is usually considered to be a *Stephanocrinus*. *Aethocystis*, S. A. Miller (1892), Silurian, Indiana, may be placed here provisionally.

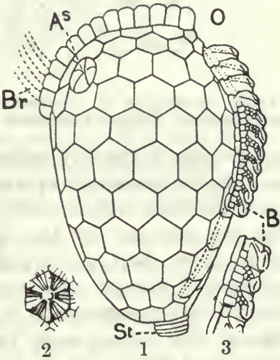


FIG. XIX.

Amygdalocystis florealis. 1, from side; 2, single plate enlarged; 3, portion of food-groove enlarged. *Br*, dotted outline of some brachioles; *Br'*, facet for attachment of same. Original, from specimen belonging to Dr. G. J. Hinde.

FAMILY 5. MALOCYSTIDAE. Rhombifera in which thecal plates are numerous and indefinitely arranged. Radial folds of stereom often pronounced, but minor rhomb-like striae not clearly seen. Food-grooves on exothecal processes passing over the theca and bearing brachioles. Columnals (when known) in a single series. This Ordovician family shows the independent evolution of a structure common in a later family, *Glyptocystidae*, viz. the extension from the mouth over the theca of series of alternating plates, supporting a single series of brachioles. The alternating series is not so complicated as in Glyptocystidae, and the food-groove passes, not on the top of it, but along its sides. The main grooves appear in all cases to be reduced to two; but these may branch and wind round the theca as in the later form, *Sphaerocystis* (p. 63), or may remain simple, and stretch in the transversal plane. Genera—*Malocystis*, Billings (1858). Chazy Limestone, Canada. Theca globular. In the type-species the grooves branch. *Amygdalocystis*, Billings (1854), Trenton Limestone, Canada. Theca (Fig. XIX.) flattened in plane of food-grooves, and elongate. Grooves never branched.

Family 6. Glyptocystidae. Rhombifera with stem, theca, and brachioles. The theca composed of five circlets of alternating plates, typically five in each circlet. In first (aboral) circlet, right posterior (r. post.) plate is always fused with right antero-lateral (r. ant.) plate. Anus, with valvular pyramid, between second and third circlets, in right posterior interradius (r. post. IR). Hydropore in adoral circlet, always opposite unpaired arm-groove, and thus defining posterior interradius (post. IR). The trans-sutural foldings of the stereom (pore-rhombs) are restricted in distribution but exaggerated in structure ("pectinirhombs").

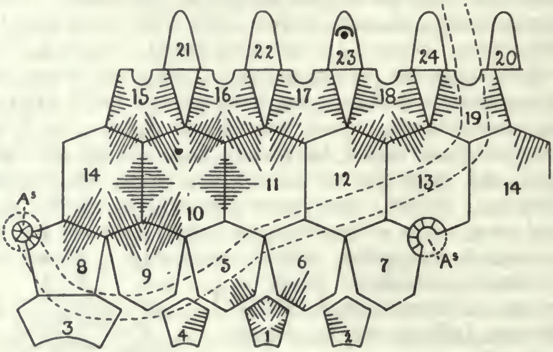


Fig. XX.

Actual distribution of pore-rhombs explained by supposed course of gut in primitive Glyptocystidae. The plates numbered as in Fig. XXI.

One of them invariably unites the left posterior plate of the first aboral row with the left anterior plate of the second row. Mouth central; from it over the theca radiate food-grooves, primitively 5, by reduction 4 or 2; these are bordered by the plates of the adoral circlet, or by plates derived from their proliferation; and these side-plates bear facets for brachioles of biserial structure. This family is perhaps descended from primitive Echinosphaeridae, in which a natural tendency to the development of five food-grooves (one ant., single; two lateral, paired) was accompanied by decrease in number, and increase in size and thickness, of the thecal plates, together with their arrangement in five alternating circlets of five (as in *Mimocystis*). The diminution of the thecal cavity, we may suppose, pressed the coil of the gut against the body wall; thus the respiratory function was hindered in the pore-rhombs along this tract, so that they disappeared, while it was thrown more on the remaining pore-rhombs, which became highly developed (Fig. XX.). The process continued till only three pair of intensely folded areas were left, one at the base on the side opposite the anus, the others above the anus to the right and left of it; from their likeness to combs, these areas are called pectinated rhombs, more shortly "pectinirhombs."

We may reconstruct a form like that analysed in Fig. XXI. as a type (probably ancestral) from which every known genus of this family may easily be derived. In this archetype two plates (r. post. and r. ant.) of the aboral circlet are fused together, so that the total number is twenty-four; numbers are attached to these in the diagram, after a plan originated by Forbes. The following statements may safely be made concerning this archetype, those applying equally to the whole family being italicised:—*3 is the double plate; a pectinirhomb joins 1 & 5*, while other pectinirhombs were probably distributed as in Fig. XX.; *the anus is in right posterior IR*, between plates 7 and 8, and below 13; it is protected by a valvular pyramid, surrounded by a ring of smaller plates; 20-24 lie between food-grooves, and are therefore interradial; the hydropore, defining the posterior interradius, is in 23, and above it is a semi-lunar pore of unknown function (genital or excretory); opposite these is the unbranched anterior food-groove, passing to plate 15; the branches of the right groove pass to 18 and 19, those of the left groove to 16 and 17; at the end of each of the five main grooves is a facet, bearing a brachiole *composed of two alternating series of ossicles* ("*biserial*"); *the food-grooves of both brachioles and tegmen are protected by small covering-plates; the theca is borne on a stem, which at its proximal end has low columnals with a wide lumen, and which tapers distally.* Modifications of this type take place in the following directions:—Enlargement of the ring of small plates around the anus, into a region of scaly, flexible integument (*Cheirocrinus*, *Glyptocystis*, *Pleurocystis*); the accentuation of the relations of the five main grooves to plates 15-19, coupled with the sinking of those plates between those of the third series (*Cheirocrinus*,

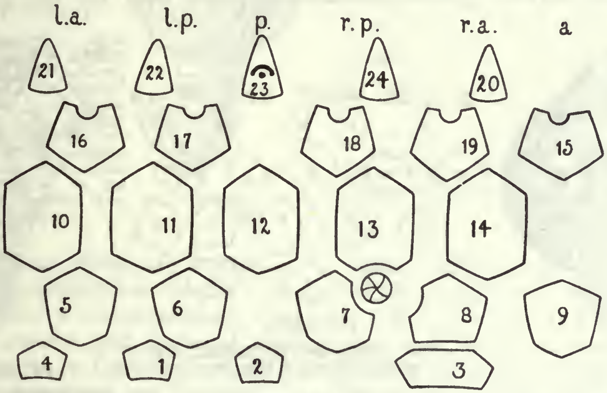


FIG. XXI.

Arrangement of plates in the supposed archetype of the Glyptocystidae. The attached numbers are those given by Forbes. The letters at the top, read from left to right, denote: left anterior interradius & radius; left posterior interradius & radius; posterior interradius; right posterior interradius & radius; right anterior interradius & radius; anterior radius. Plate 23 bears the hydropore and gonopore; the notches in plates 15 to 19 represent the primitive position of five food-grooves; between 7, 8, and 13 lies the anus. Pectinirhombs not shown.

Cystoblastus); the extension of the subvective system over the thecal plates, by the proliferation from plates 20-24 of alternating series of plates, in which every other plate bears a brachiole (*Schizocystis*, *Glyptocystis*, *Lepadocystis*, *Callocystis*, *Sphaerocystis*, *Lepadocrinus*, *Pseudocrinus*); the atrophy of the anterior groove (partially in *Glyptocystis*, more so in *Prunocystis* and *Schizocystis*, wholly in *Lepadocrinus*, *Sphaerocystis*, and *Strobilocystis*); atrophy of two side grooves in addition (*Schizocystis*, *Pseudocrinus*, *Pleurocystis*); restriction of pectinirhombs to sutures between 1 & 5, 14 & 15, and 12 & 18 (*Prunocystis*, *Schizocystis*, *Pseudocrinus*, *Lepadocrinus*, *Callocystis*). None of these characters can be taken as a basis of classification; each group so formed would include genera very diverse in other respects; doubtless the same structures have in many cases been independently attained. Happily certain relationships seem clear, and round them the genera may be gathered into sub-families.

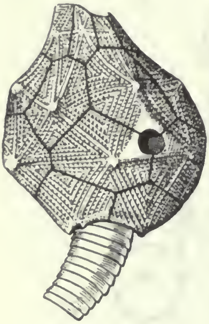


FIG. XXII.
Echinoencrinus Senckenbergi, after Jaekel.

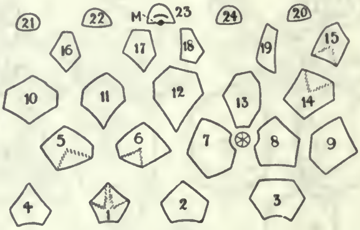


FIG. XXIII.
Analysis of *Echinoencrinus*, original, after specimen E1265 in Brit. Mus.

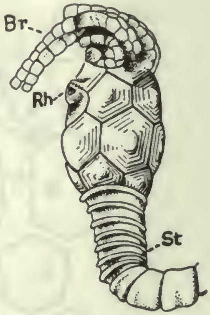
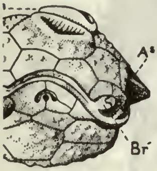


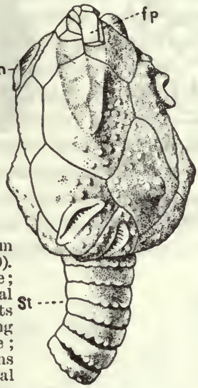
FIG. XXIV.
Prunocystis Fletcheri (from Brit. Mus., 40207). *Rh*, pectinirhomb. × 4 diam.

SUB-FAMILY 1, ECHINOENCRININAE, passes from the simple form *Echinoencrinus*, in the direction of extension of two of the lateral grooves over the theca, through *Prunocystis* to *Schizocystis*; pectinirhombs 1 & 5 and 14 & 15 always, 12 & 18 frequently present, but no others, except 1 & 6 in *Echinoencrinus*. Genera—*Echinoencrinus*, H. v. Meyer (1826; synn. *Gonocrinus*, Eichwald, 1840, and *Sycocystis*, von Buch, 1845; see also Volborth, 1842), Ordovician, Russia, differs from the imagined archetype in restriction of pectinirhombs to 1 & 5, 1 & 6, and 14 & 15, and in apparent bisection of plate 23 (Fig. XXIII.). The main grooves may support five brachioles, or only two, or may branch yet more; in any case the facets are always close around the mouth. Anal region often prominent (*Erinocystis*, Jaekel, 1899). The plates usually have strong radiating folds, often crossed by finer concentric ridges (Fig. XXII.). Here Jaekel (1899) places his *Glaphyrocystis* and *Scoliocystis*, Ordovician, Russia. *Prunocystis*, Forbes (1848), Silurian, England, includes *P. Fletcheri* and *Echinoencrinus baccatus*, Forbes (Fig. XXIV.). Theca "shaped like the fruit of a dog-rose." Adoral row of plates increased in number. Pectinirhombs on 1 & 5, 14 & 15, and 12 & 18 only.

Brachioles clustered round mouth, probably five, slender, and comparatively long. *Schizocystis*, Jaekel (1895), Silurian, England. Type, *Echinoencrinus armatus*, Forbes (Figs. XXV.-XXVII.). Arrangement of plates and rhombs as in *Prunocystis;* rhomb 12 & 18 sometimes absent. Ant., r. ant., and l. post. food-grooves almost or entirely atrophied ; l. ant. groove extends nearly half-way down the theca on to plate 11, is floored with alternating plates, bears about five brachioles ; a similar extension of r. post. groove to plate 13 is checked by anus, and bears only three brachioles. Sub-Family 2, Callocystinae, starts from a form in which all five subvective grooves, with the usual flooring plates and brachioles, pass over the theca, as in *Lepadocystis;* and diverges (*a*) by suppression of grooves, without branching, into *Lepadocrinus* and *Pseudocrinus;* (*b*) by branching of grooves, with subsequent suppression, into *Callocystis*, *Sphaerocystis*, and *Strobilocystis;* pectinirhombs 1 & 5, 14 & 15, 12 & 18 probably always present. Genera — *Lepadocystis*, P. H. Carpenter (1891 ; syn. *Meekocystis*, Jaekel, 1899), Ordovician, Indiana (Fig. XXVIII.). Theca ovoid; plates around anus slightly altered from the archetypal position. Pectinirhombs on 1 & 5, 12 & 18, 14 & 15, and 10 & 15. Main grooves five, stretching a short distance over theca, one to each plate of fourth circlet. *Lepadocrinus*, Mather (1843 ?; Conrad, 1840 ; Hall, 1859 : synn. *Apiocystis*, Forbes, 1848 ; *Staurocystis*, Haeckel, 1897 ; ? *Hallicystis*, Jaekel, 1899 ; includes



XXV.



XXVI.

IGS. XXV. & XXVI.

chizocystis armatus (from . Mus., E7589 & E7590). . XXV. from above; VI. from the abanal . *As*, anus ; *Br'*, facets brachioles ; *fp*, flooring es of subvective groove ; ig. XXVI. the impressions hese are seen in the distal part of the groove ; *Rh*, the pectinirhomb of plates 14 & 15 ; *St*, part of stem.

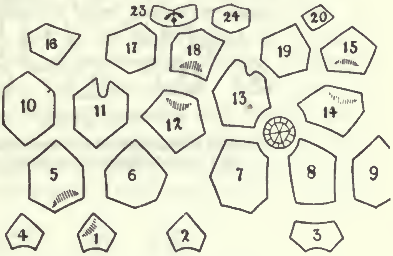


Fig. XXVII.

Analysis of *Schizocystis.* Plates 11 & 13 are notched by the food-grooves. Plate 23 is double, and bears hydropore and gonopore.

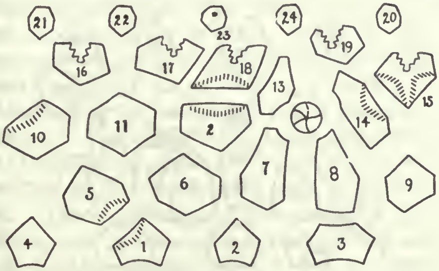


Fig. XXVIII.

Analysis of *Lepadocystis Moorei*, based on Meek's figures (1871 & 1873). Plates 15 to 19 notched by food-grooves ; hydropore on plate 23.

Pseudocrinus quadrifasciatus and *P. oblongus*), Silurian, North America, England, Scandinavia (Fig. XXX.). Plates much as in *Lepadocystis.* Pectinirhombs on 1 & 5, 12 & 18, 14 & 15 only. Main grooves four, the anterior being aborted, extend over theca to a degree that differs in different species, and is always less in younger stages. *Pseudocrinus,* Pearce (1842, redescr. Forbes, 1848), Silurian, England (Fig. XXIX.). Resembles a *Lepadocrinus* in which all main grooves are aborted except apparently r. post. and l. ant. The grooves are the same as those of *Schizocystis,* but their relation to the thecal plates and anus is as in *Lepadocrinus.* The theca is compressed so as to have two almost flat oval sides, fringed by the brachioles of these grooves; one side contains the anus and pectinirhomb 14 & 15, the other contains pectinirhombs 1 & 5, and 12 & 18. *Callocystis,* Hall (1852, syn. *Anthocystis,* Haeckel), Silurian, North America (Fig. XXXI.). Plates 10, 12, and 14 are sunk down between 6 and 7, 8 and 9 respectively, so as to rest on 2 and 3; thus there appear to be eight plates in the second circlet. Contrariwise, by the vertical elongation of 7 and 8, 13 is raised between 18 and 19. The remaining plate of the third

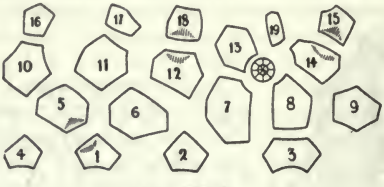


FIG. XXIX.

Analysis of *Pseudocrinus,* based on specimens in the British Museum, especially 40193.

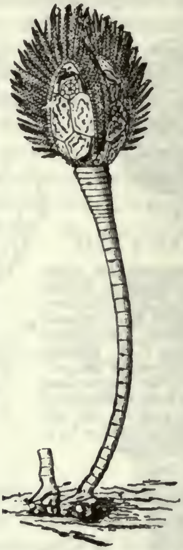


FIG. XXX.

Restored *Lepadocrinus quadrifasciatus.* The armlets of the outer rows are erect; those of the middle row depressed. Near the top of the left-hand quarter is the anus; near the top of the right-hand quarter is a pectinirhomb. By permission of the Keeper of the Geological Dept., British Museum.

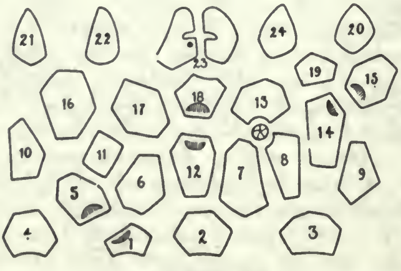


FIG. XXXI.

Analysis of *Callocystis Jewetti* based on Hall's figures.

circlet is reduced in size and sometimes quite atrophied. Pectinirhombs on 1 & 5, 12 & 18, 14 & 15, as usual. Main grooves five, pass nearly to base of theca; one or more of the grooves may bifurcate once towards the distal end. *Sphaerocystis*, Hall (1859), Silurian, Maryland. Theca spheroidal. Main grooves four, each with three to six branches. Plates undetermined; pectinirhombs, anus, and hydropore situated as in *Lepadocrinus*. *Strobilocystis*, White (1876), Devonian, Iowa, resembles *Sphaerocystis*, but the branches have become "small secondary arm-grooves extending obliquely downward from each side of the principal grooves." Sub-Family 3. Glyptocystinae. Besides the negative characters of irregularity in the shape of the plates and in the distribution of pectinirhombs, the only feature common to the included genera is the evidence they offer of descent from a simple form like *Cheirocrinus*. The number of pectinirhombs connects *Cheirocrinus* with *Cystoblastus* and *Glyptocystis*; the enlargement of the anal area connects it with *Glyptocystis* and *Pleurocystis*; the relation of the third circlet of plates to the fourth is another link with *Cystoblastus*. Genera—*Cheirocrinus*, Eichwald (1856 and 1859; see also Schmidt, 1874, under *Glyptocystis*), Ordovician, Russia, and North America. The chief departures from the archetypal arrangement of plates are correlated with an increase in size of the anal area, which is covered with numerous small plates, and surrounded by plates 7, 8, 12, 13, and 14. This in *C. penniger*, the type-species, induces the vertical fission of 18 (or intercalation of 18*a*), and sinking of 12 on to 2; the pushing of 15 to the right over 10, and sinking of 10 between 9 and 5 on to 4; the pushing of 17 to the left over 11; the consequent sinking of 16 between 10 and 11 on to 5. In *C. Volborthi* the plates of the third row are not sunk, but raised between those of the fourth row; this is a change in the direction of *Cystoblastus*. The distribution of the numerous pectinirhombs varies with the species, and, to some extent, with the individual; those on 1 & 5, 1 & 6, with the demi-rhombs 1 & 4, 1 & 2, are constant. The arrangement in one specimen of *C. penniger* is shown in Fig. XXXII. Reversions to the older and simpler type of rhomb structure occasionally occur (*e.g.* 13 & 18*a* in the figure). The five main grooves pass between plates 20-24 to plates 15, 16, 17, 18*a*, and 19; they are rather wide and fringed with short brachioles. The threefold division of

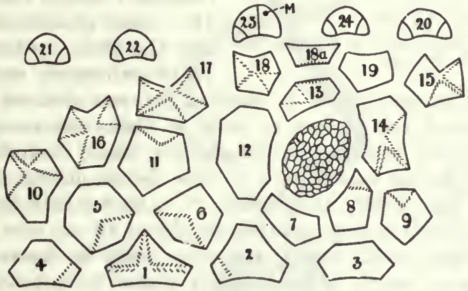


Fig. XXXII.
Analysis of *Cheirocrinus penniger*, modified from Fr. Schmidt.

plates 20-24 in *C. penniger* is the first stage in the proliferation of those plates to floor the food-grooves; more advanced stages occur in other species, thus leading to *Glyptocystis*. *Homocystis*, Barrande (1877), Ordovician and Silurian, Bohemia, resembles *Cheirocrinus* in the shape of the theca, the number of pectinirhombs, and the position of the anus. The material does not permit more precise comparison. *Glyptocystis*, Billings (1854 and 1858), Ordovician, Canada. Theca ovoid (Fig. XXXIII.). Anal area less large than in *Cheirocrinus*, enclosed by 8, 13, and 14. Plate 16 sunk on to 5, as in *C. penniger*; thus 11 is pushed to the right, and both 11 and 12 are reduced in size. Pectinirhombs 1 & 5, 1 & 6, 10 & 14, 10 & 15, 13 & 17, 15 & 16, 16 & 17, 17 & 18, 18 & 19; demi-rhomb 10 & 16; imperfect rhombs, 7 & 8, 11 & 12, 15 & 19. Main grooves five, passing over the theca, by way of plates 15-19; all nearly reach the base except anterior groove, which is checked by pectinirhomb 10 & 15. The resemblance of the grooves to those of Callocystinae suggests that that sub-family was derived from *Glyptocystis* itself; but this is negatived by the different modification of the thecal plates. *Pleurocystis*, Billings (1854 and 1858), Ordovician, N. America and Britain (Fig. XXXIV.). Anal area so large as to occupy almost all one side of the theca with its numerous small plates, the anus being at lower right-hand corner of the area, which is bordered by plates 3, 2, 7, 12, 13, 14, 8. Correlated with this is a flattening of the theca in l. post. and r. ant. plane, the atrophy of all main grooves except the two in that plane, great diminution in size of plates 15-19, as well as 13. Pectinirhombs 1 & 5, 11 & 12, 10 & 14; the two latter are analogous to, not homogenetic with, pectinirhombs 12 & 18, 14 & 15, in *Callocystinae*. Each main groove ends in a single long and sturdy brachiole, of the usual biserial structure, with stout covering-plates. The stem is longer than usual in the family. The curious homoplastic resemblance to the Anomalocystidae (p. 52) led Haeckel to place *Pleurocystis* in that family, though it differs in every essential structure. *Cystoblastus*, Volborth (1867 and 1870), Ordovician, Russia (Fig. XXXV.). Imagine a *Cheirocrinus* in which plates 10, 11, 12, and 14 are still further pushed up between those of the fourth circlet than they are in *C. Volborthi*, in which plate 13 has entirely disappeared so as to compensate for the asymmetry induced by the anus; in which the arm-grooves, of the usual structure, are stretched well into plates 15-19 and limited to those plates, as in *C. sculptus:* then you will have such a form as *Cystoblastus*. It need only be added that the anus is surrounded by plates 8, 14, and 19; and that pectinirhombs 1 & 5, and 1 & 6 remain as before, while demi-rhombs unite the plates

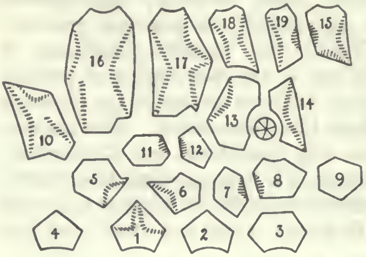


Fig. XXXIII.

Analysis of *Glyptocystis multiporus*, modified from E. Billings.

which now form the third circlet, viz. in order, 14, 15, 10, 16, 11, 17, 12, 18, 19. The superficial resemblance of *Cystoblastus* to certain Blastoids has led most writers to imagine a true relationship. This involves the entire disappearance of plates 5-9; the homologising of the plates here called 10, 11, 12, and 14, as well as the absent 13, with plates 20-24, and the consequent disappearance of plates 10-14 also; the violent supposition that the horizontal transverse or tangential folds of the demi-rhombs in *Cystoblastus* originated the radial or vertical folds of the hydrospires in *Codaster;* as well as such minor points as the shifting of both anus and hydropore, and the fusion of two pair of basals, neither of them the same pair as composes plate 3 of *Cystoblastus.*

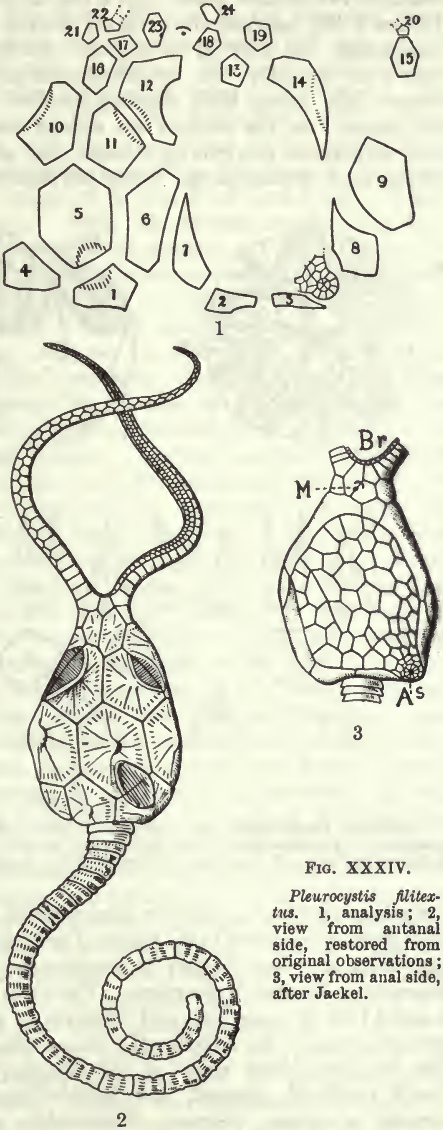


Fig. XXXIV.

Pleurocystis filitextus. 1, analysis; 2, view from antanal side, restored from original observations; 3, view from anal side, after Jaekel.

The structures of the subvective grooves in the more highly specialised genera of this family have often been spoken of as "recumbent arms." They differ, however, from the arms of Crinoidea in origin as well as recumbency. From the subvective structures of Glyptosphaeridae and Protoblastoidea, they differ in that the brachioliferous plates are not thecal plates or even intercalated between such plates, but lie outside them and often transgress their sutures.

FAMILY 7. CARYOCRINIDAE. Rhombifera in which the theca is composed primitively of four circlets of plates, comparable to the infrabasal (IB), basal (B), radial (R), and deltoid (Δ) circlets of a crinoid with dicyclic base (p. 99), and dominated by trimerous symmetry. IBB 4, the two on either side the anal interradius apparently being produced by fusion of two original pairs. BB 6 (ten in *Heterocystis*). Alternating with BB are 6 RR, between which, on the anterior side of the cup, two or three interradials (iR) may be developed. (In *Heterocystis* the iRR also alternate with the BB.) On the interior of all these plates the stereom is thrown into strong folds, forming bundles of laminae at right angles to the sutures; on the exterior the ends of the folds are marked by pores, each surrounded as a rule by a raised rim, and sometimes broken up into two or more smaller pores. Since the laminae correspond in position and essential structure to ordinary pore-rhombs, the pores necessarily run in lines from the umbones to the angles of each plate (Fig. XXXVI. 3, 4); these structures may have helped in respiration; but are in no sense homologous with Blastoid hydrospires. The three primitive food-grooves (ant., r. and l.) are of equal size and bifurcate in like manner. The proximal portion tends to be hypothecal; then a short portion lies on the theca like the "recumbent arms" of the Glyptocystidae; the distal portion is freely exothecal, biserial, and brachioliferous. Stem well developed, circular in section. Genera—*Hemicosmites*, von Buch (1840, redescribed 1845; see also Joh. Müller, 1854; syn. *Hexalacystis*, Haeckel), Lower to Upper Ordovician, Russia, and perhaps Silurian, N. America. Comparing the dorsal cup (Fig. XXXVI. 3) with a crinoid cup, we may

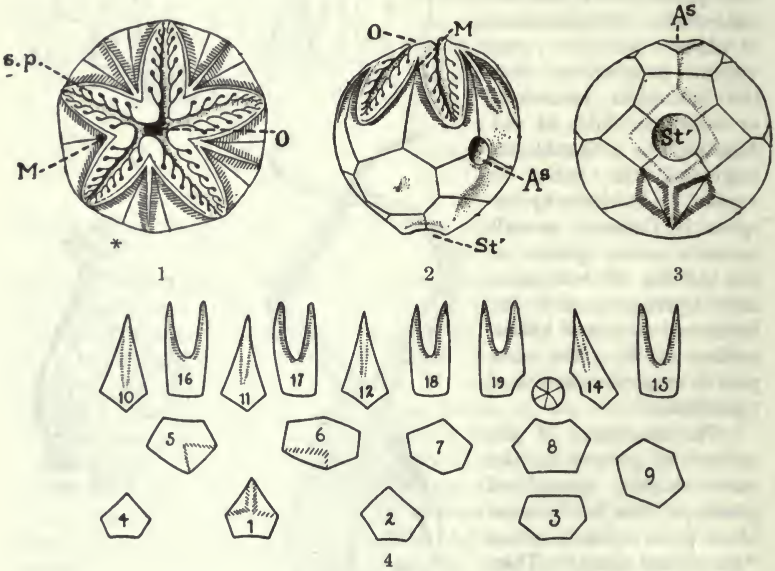
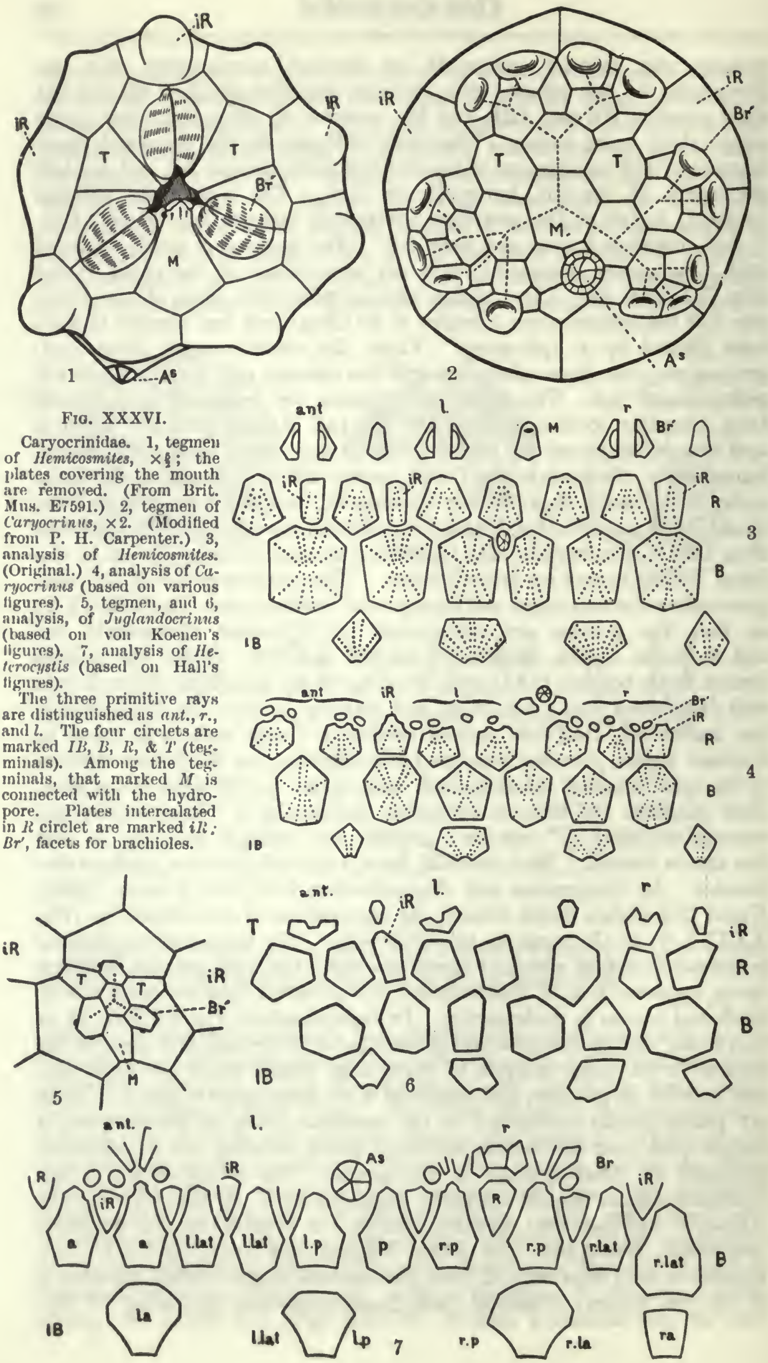


FIG. XXXV.

Cystoblastus Leuchtenbergi, after Volborth. 1, oral surface; 2, posterior; 3, aboral surface; 4, analysis; *s.p*, plates flooring arm-grooves; *O*, mouth; *As*, anus, the position of which is indicated by * in 1; *M*, hydropore between 18 & 19; *St'*, attachment of stem.

imagine the anterior radius to be doubled, concurrently with the bifurcation of the anterior arm, and may therefore speak of the left and right anterior RR and IBB and the anterior B, while the other plates retain their usual names. The three iRR rest on the truncated upper margins of the anterior and right and left antero-lateral BB, and are half the width of the RR, but quite as high. The anus, with valvular pyramid, is left of the posterior interradius, being in fact below l. post. R, and between l. post. and post. BB. The tegmen is solidly covered with nine plates alternating with the nine plates of the radial circlet (Fig. XXXVI. 1). These plates have no pores like those of the dorsal cup (but the posterior one is rugose at its adoral end, and appears to have been pierced by a hydropore). From the central mouth three food-grooves run over these plates towards the anterior and the right and left antero-lateral RR. The mouth and grooves are protected by relatively large irregular covering-plates. At the end of each groove is an oval area over which passed the base of a biserial arm, which became free almost immediately. *Caryocrinus*, Say (1825, see von Buch, 1845, and Hall, 1852; synn. *Stribalocystis*, S. A. Miller; *Enneacystis*, Haeckel), Upper Ordovician, Scandinavia, and Silurian, N. America. Dorsal cup (Fig. XXXVI. 4) differs from that of *Hemicosmites* only in absence of anterior iR, and of anus, the latter having moved up to the tegmen. The covering-plates of the food-grooves have become larger and incorporated in the tegmen (Fig. XXXVI. 2), so that the grooves are subtegminal (cf. Crinoidea Camerata); but end in facets on the margins of the RR and iRR. Since the grooves branch while beneath the tegmen, these facets are more than three, though still distributed into a left, right, and anterior group. In the growth of the individual, Hall has noticed successive stages with from three to fourteen facets; six and nine are fairly common, but for adults thirteen is the usual number, the thirteenth being added on the right of the anus. Hall describes the arms as composed proximally of "semicircular, and scarcely interlocking" ossicles; distally the brachials alternate so that the arm is biserial. Each brachial bears a grooved pinnule, perhaps also biserial. In *Corylocrinus* and *Juglandocrinus* (both von Koenen, 1886), Upper Ordovician, South France, the composition of the dorsal cup (Fig. XXXVI. 6) is the same as in *Caryocrinus*. The tegmen of *Corylocrinus* is composed of four plates, of which the right, left, and anterior bear arm facets, apparently as in *Hemicosmites;* the posterior tegminal plate is very thick and porous (a madreporite). In *Juglandocrinus* (Fig. XXXVI. 5), as in a young *Caryocrinus*, the food-grooves are subtegminal, and come to the surface on the upper margins of three large plates, which are right, left, and anterior in position, and alternate with three smaller plates. These six plates exactly correspond to the tegminal plates of *Hemicosmites;* a central plate over the mouth, and three plates covering the food-grooves, represent the covering-plates of that genus. This interpretation of von Koenen's obscure genera was partly suggested by P. H. Carpenter (1891). An anus was doubtless present, though not observed in the imperfect specimens. *Heterocystis*, Hall (1852), Silurian, New York (Fig. XXXVI. 7), appears to have been derived from *Hemicosmites* by the vertical bisection of 4 BB (viz. r. post., r. ant.-lat., ant., l. ant.-lat.), thus producing 10 BB;



iR
T
M
Br′
Aˢ
1
iR
T
M.
Br′
Aˢ
2
ant
l.
r
M
Br′
iR
R
B
IB
3
ant
iR
l
r
Br′
iR
R
B
IB
4
T
iR
Br′
M
5
ant.
l.
r
T
iR
R
B
IB
6
ant.
l.
r
R
iR
As
Br
a
a
l.lat
l.lat
l.p
p
r.p
r.p
r.lat
r.lat
B
IB
la
l.lat
l.p
r.p
r.la
ra
7

Fig. XXXVI.

Caryocrinidae. 1, tegmen of *Hemicosmites*, $\times\frac{3}{2}$; the plates covering the mouth are removed. (From Brit. Mus. E7591.) 2, tegmen of *Caryocrinus*, ×2. (Modified from P. H. Carpenter.) 3, analysis of *Hemicosmites*. (Original.) 4, analysis of *Caryocrinus* (based on various figures). 5, tegmen, and 6, analysis, of *Juglandocrinus* (based on von Koenen's figures). 7, analysis of *Heterocystis* (based on Hall's figures).

The three primitive rays are distinguished as *ant.*, *r.*, and *l.* The four circlets are marked *IB*, *B*, *R*, & *T* (tegminals). Among the tegminals, that marked *M* is connected with the hydropore. Plates intercalated in *R* circlet are marked *iR*; *Br′*, facets for brachioles.

the corresponding broadening of l. ant. B; the sinking of the 6 RR, and 3 iRR, so as to alternate with the 10 BB, except in posterior IR, which is entirely occupied by anal plates; the repeated bifurcation of the arms, as in *Caryocrinus*, but probably to a greater extent, accompanied by an increase in number of tegminal and accessory plates, the arrangement of which is unknown. Stereom-folds are visible. Thecal plates nodose (cf. *Hemicosmites*), hence the name of *H. armatus* given to the only specimen known.

Throughout this family there is no strict correlation between the arms and the cup-plates. There is in both structures a dominance of the number three or six, it is true; but each arm has not its own radial plate supporting it, as in Crinoidea. Indeed, an arm may be borne by a plate that, on all other grounds, would be considered as interradial. Moreover, the trend of evolution in the family is parallel to the probable evolution of early Camerata, rather than towards that or any other Crinoid type.

Order 3. **Aporita**, Zittel (1879, restr.)

Cystidea in which pentamerous symmetry affects the food-grooves and thecal plates, probably also the nerves and ambulacral vessels, but not the gonads. The food-grooves are exothecal and circumoral. The stereom and stroma show no trace of folds, rhombs, diplopores, or anything other than the finely porous structure characteristic of all Echinoderm stereom.

One may regard this order as a backwater in the stream of progress, derived perhaps from the Rhombiferi, but leading nowhere in particular, and only retained because the forms referred to it cannot be placed elsewhere. The arrangement of the thecal plates, and a homoplastic resemblance to *Hypocrinus* (p. 178), have suggested to some a connection with the Crinoidea.

There is only one family, the Cryptocrinidae, and in it the thecal plates are arranged in four circlets. *Cryptocrinus*, von Buch (1840 and 1845), Ordovician, Russia (Fig. XXXVII.). Theca small, irregularly spheroidal, composed of four circlets of plates. Aboral circlet of three unequal plates, produced by fusion of an original five, the unfused plate being in right anterior interradius. Above these is a circlet of five rather large hexagonal plates, following on and alternating with which are five smaller sub-pentagonal plates. These surround an irregular pentagon in which are the minute plates of the fourth circlet, and other small tegminal plates. Five main food-grooves lead from the mouth to facets borne by these adoral plates. The free brachioles rising from the facets must have been slender. The anus, with valvular pyramid, lies between two plates of the third circlet, either supported on a plate of the second circlet, or separated therefrom by a small supplementary plate. The hydropore appears to have been in the adoral plate opposite the anterior food-groove, and left of the anus, which therefore occupies much the same position as in Glyptocystidae. Another pore, perhaps excretory, lay in the adoral plate on the left, that is, opposite the anus. There was a slender stem of circular columnals. *Lysocystis*, S. A. Miller (1889, proposed for *Echinocystis*, Hall *non* Wyville Thomson; syn. *Scolocystis*, Gregory, 1897), Silurian, N. America. Theca sub-pentagonal, composed of four circlets of plates. Aboral circlet of four (?) small plates, followed by two circlets of five plates each, regularly alternating, and an adoral circlet, number unknown. Apparently three free brachioles, possibly becoming five by the usual bifurcation. Anus at adjacent upper angles of two plates of third circlet. In the only known species the plates of second and third circlets were strongly nodose. Stem unknown.

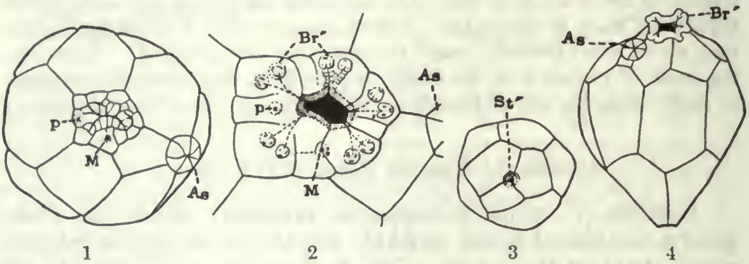


FIG. XXXVII.

Cryptocrinus. 1, from oral surface; 2, enlarged view of oral region, the tegminal plates removed; 3, aboral view; 4, side view. (All diagrammatised from Jaekel.) *As*, anus; *Br′*, facets for brachioles; *M*, hydropore; *p*, another pore; *St′*, facet for stem.

ORDER 4. **Diploporita**, Zittel (1879, emend.)

Cystidea in which radial symmetry affects the food-grooves, and by degrees the thecal plates connected therewith, but not the interradial thecal plates; probably also the nerves and ambulacral vessels, but not the gonads. The food-grooves are epithecal, *i.e.* are extended over the thecal plates themselves without intermediate flooring; they are also prolonged on to exothecal brachioles, which line the epithecal grooves. The stereom of the thecal plates may be thrown into folds, but the mesostroma does not so much tend to lie in strands traversing the sutures, nor are pectinirhombs or "pore-rhombs" developed; diplopores are always present in the mesostereom, but often restricted to definite tracts or plates, especially in higher forms.

While some descendants of the Aristocystidae were seeking in vain to perpetuate their race by assuming the flattened carapace of Anomalocystidae, and while others, becoming more reconciled to a sedentary life, were stretching out from their mouths longer and longer arms into the food-bearing sea, raising themselves too on loftier columns, there were yet others that hit upon another way of meeting the needs of a fixed existence. The chief need was to expose food-collecting surface in greater amount and over a wider area. The way found was to stretch ciliated grooves from the mouth over the surface of the theca, and then to raise them on armlets or brachiola placed at fit intervals. At the same time, the hydrocoel, it may be inferred from its constant connection with such grooves, sent out branches corresponding with the food-grooves; from these branches were given off the podia, serving for both respiration and the prehension of food. This wandering of the brachiola away from the mouth marks then the development of two structures previously unknown among Echinoderms: (1) canals radiating from the hydrocoel along the theca; (2) an intrabrachial, circumoral, or ventral region of the theca, such as in Crinoids is called the tegmen. These two structures, in one form or another, characterise all Echinoderma other than Amphoridea and a few Rhombiferi. But it seems that they were independently developed along many lines. What in the Crinoidea is a mere "tegmen" or pot-lid, comes in *Glyptosphaera*, in the Edrioasteroidea, and in the Echinoidea, to form the greater part of the test; and with it the perradial ambulacral vessels extend; whereas the theca of Aristocystidae, which in Crinoidea becomes the specialised and important calyx or dorsal cup, is in the other orders more and more reduced until in some cases no more of it can be recognised than the plates of the anal pyramid or their homologues. Another structure characterising this order, viz. diplopores (p. 41), may possibly have assisted respiration by bringing lacunar blood-vessels into closer contact with the sea-water; this may have been connected with a less development of podia. The functions of diplopores have not as yet been satisfactorily explained by reference to recent Echinoderms.

FAMILY 1. SPHAERONIDAE. Primitive Diploporita, in which the food-grooves do not extend from the mouth beyond the adoral circlet of plates. Diplopores diffuse. The included genera show the early stages of tegminal and ambulacral development; in none of them does more than a single cycle of plates intervene between the oral pole and the bases of the brachiola. The five plates forming the cycle are interradially placed, being separated by the grooves proceeding from the mouth to the brachioles. The direction of these grooves is primitively the same as that of the food-grooves in *Echinosphaera*, viz. one anterior, opposed to the anus, two lateral, each of which soon branches, thus making five grooves in all, with bilateral symmetry. Thus the shape and position of the five intervening plates are those characteristic of true orals (see p. 124). Genera—*Sphaeronis*, Hisinger (1828 and 1837); the name was proposed to replace *Echinosphaera* of Wahlenberg (1818) for no assigned reason, but was restricted to forms agreeing with *Echinus pomum*, Gyllenhal, by Joh. Müller (1854). The species referred to this genus by Angelin (1878) are all Ordovician, and agree in the following characters (Fig. XXXVIII.):—A spheroid or ovoid theca, sessile on a broad base, composed of irregular plates, the mesostereom of which is pierced by regularly formed diplopores ; the anus close to the peristome, and with a valvular pyramid ; small hydropore, perhaps combined with gonopore, between mouth and anus, to the left ; five orals separated by food-grooves with primitive bilateral arrangement. The various species may be arranged in groups, according to the number of times the grooves branch, and the number of brachiola given off from them. Haeckel (1896) has sought to separate as genera (*Pomonites*, *Pomocystis*, *Pomosphaera*) those with one, two, three, and four brachiola to each ray ; but until Angelin's notoriously inaccurate figures shall have been corrected by observation instead of by hypothesis, these names can rest on no sure ground. Moreover, Lovén's figure of the type-species, *S. pomum*, reproduced in our Fig. XXXIX., shows that the number of branches visible may be two, three, or four in a single individual. ***Eucystis***, Angelin (1878), Ordovician, Sweden (Fig. XL.), sends its grooves farther down the theca than *Sphaeronis*, over one or two circlets of thecal plates. From the distal end of each ray a brachiole was given off, while others of uncertain number and position arose along the side of the grooves. Probably some of the forms described by S. A. Miller as *Holocystites* should be placed here (e.g. *Trematocystis*, Jaekel), although their orals are not known. *H. gyrinus*, Miller & Gurley (1894), presents a stage in the development of food-grooves that in some respects is more advanced, although the peristomial plates have no regular arrangement (Fig. XLII.). *Allocystis*, Miller (1889),

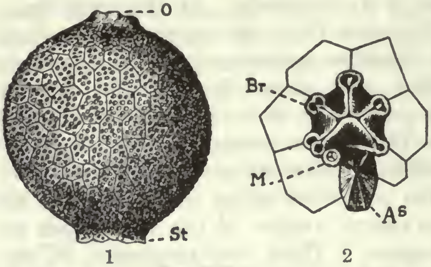


FIG. XXXVIII.

Sphaeronis globulus, after Angelin. 1, from side, nat. size ; 2, tegmen, enlarged.

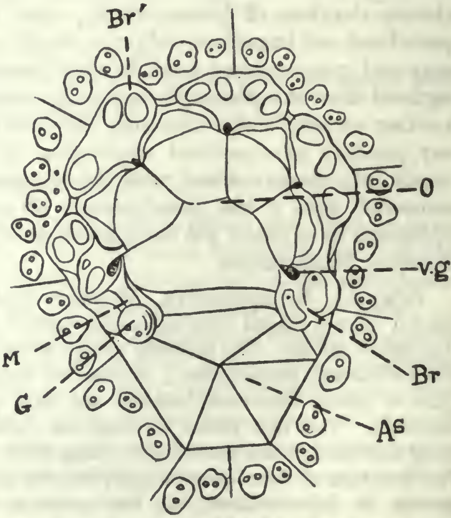


FIG. XXXIX.

Adoral region of *Sphaeronis pomum* (from Lovén, "Om *Leskia mirabilis*," *Öfv. Vet.-Akad. Förhandl.* 1867, p. 434). *O*, orals covering mouth ; *vg*, section of food-groove running from mouth to *Br′*, brachiole-facets, some of which are pierced by an axial canal ; *As*, plates closing over anus ; *G*, prominence with two pores, which Lovén considered gonopores ; *M*, ridge which Lovén thought might indicate a madreporite (or *G* may represent combined gonopore and hydropore) ; diplopores surround the whole area.

Silurian, Indiana, may go here. *Proteocystis*, Barrande (1887), Lower Devonian, Bohemia (Fig. XLI.), differs from *Sphaeronis* mainly in the irregular branching of the food-grooves, which stretch farther over the theca, though whether the tegmen ever contained more than one cycle of plates cannot be determined from the published figures. Apparently the hydropore formed a slit between the small gonopore and the mouth ; and the base, broader than in *Sphaeronis*, is said to have been prolonged into a stem.

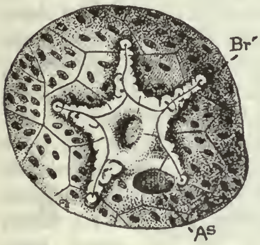


FIG. XL.
Eucystis raripunctata, oral surface, after Angelin, enlarged.

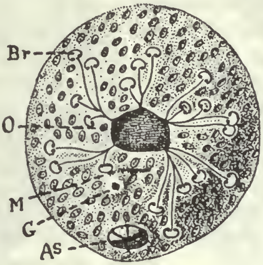


FIG. XLI.
Proteocystis flava, oral surface, slightly restored from Barrande, enlarged.

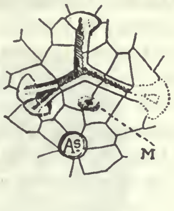


FIG. XLII.
Mouth and food-grooves of "*Holocystites*" *gyrinus*, after Miller & Gurley.

Its geological age forbids us to regard *Proteocystis* as a link between Sphaeronitidae and Glyptosphaeridae, but it certainly has points of likeness to the latter family. *Carpocystis*, Oehlert (1887), Lower Devonian, W. France, is a simple spheroid with large stem-attachment. *Palmacystis*, Haeckel (1896), *Archegocystis*, & *Codiacystis*, Jaekel (1899), are forms with the epithecal branched food-grooves, described by Barrande as *hydrophores palmées* of *Pirocystis*, *Craterina*, & *Aristocystis*.

FAMILY 2. GLYPTOSPHAERIDAE. Diploporita in which the food-grooves extend over the theca well beyond the adoral circlet, and irregularly transgress the sutures between the thecal plates. Diplopores diffuse. These represent a further advance on the type of structure originated in Sphaeronitidae. Genera — *Glyptosphaera*, J. Müller (1854), Ordovician, Baltic countries (Fig. XLIII.), has for type the species first figured by the Duke of Leuchtenberg (1843), and distinguished by Volborth (1846) as *Sphaeronites Leuchtenbergi*. The spherical theca, reaching a diameter of 7 cm., and larger than any other cystid, is composed of irregularly arranged polygonal plates, bearing diplopores. The mouth is covered by five orals (O) with characteristic bilateral symmetry, and from between them the anterior unpaired, and lateral paired, grooves radiate about

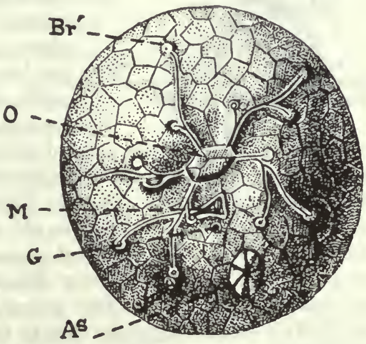


FIG. XLIII.
Glyptosphaera Leuchtenbergi, after Volborth, nat. size. For lettering, see adjoining text.

half-way over the theca, crossing the sutures of the plates, and giving off short branches on either side, or sometimes on one side only, at irregular intervals. At the ends of the branches are facets (*Br′*) for the support of brachioles. The grooves are shallow and have minute covering-plates. The anus (*As*), of which the valvular pyramid is rarely preserved, lies about a third of the way down the theca; between it and the mouth are two openings, a little to the left, viz. a small round gonopore (*G*) and a madreporite (*M*). The latter, the representative of the hydropore, is always close to the first brachiole-facet of the left posterior groove, at the junction of three plates; it consists of folds (slits ?) running at right angles to the sutures, and is bounded by a slight ridge forming a triangle or trapezoid. According to Volborth, there was at the aboral pole a stem, $\frac{1}{10}$ to $\frac{1}{6}$ width of theca, with a wide lumen, and low columnals with five longitudinal sutures, and with encrusting root-expansion. Eichwald, however, could not find more than a short conical extension of the theca, and this agrees better with the appearances of specimens sent by Volborth to the British Museum.

Fungocystis, Barrande (1887), Ordovician, Bohemia (Fig. XLIV.), differs from *Glyptosphaera* in the broad base, hollowed for attachment to some marine object, and forming an angle with the long axis of the theca; the paucity of diplopores; and the regular alternation of the groove branches, making each groove a zigzag. The test itself is not preserved; the internal casts show no sign of the external grooves and brachioles; but they show between anus and mouth a curved elevation (madreporite ?).

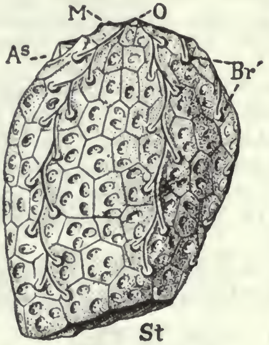


Fig. XLIV.

Fungocystis rarissima, reconstructed on the evidence of Barrande's figures; enlarged.

Family 3. Protocrinidae. Diploporita in which the food-grooves extend over the theca almost to the aboral pole, and are regularly bordered by alternating thecal plates ("adambulacrals"), on which are the brachiole-facets. Diplopores diffuse or confined to adambulacrals, from which they are never absent. These represent a further advance in precisely the same direction as previous families. Genera—*Protocrinus*, Eichwald (1840), Ordovician, Russia (Fig. XLV.), was well described by Volborth (1846). Theca spheroidal or ovoid, attached by a stem in the young, but free in old age and losing all traces of attachment (cf. *Lichenoides*). Thecal plates larger, stouter, and more swollen than in *Glyptosphaera;* all bear diplopores, which may become somewhat at right angles to main food-groove, on the adambulacrals. The main grooves are rather straighter than in *Glyptosphaera*, lying regularly between large alternating thecal plates (adambulacrals), each of which bears a brachiole, except one or two of the proximal ones on the side towards the direction of the clock-hands. Hydropore minute, above anus. *Proteroblastus*, Jaekel (1895; syn. *Dactylocystis*, 1899), Ordovician, Russia (Fig. XLVI.). Theca ovoid, sometimes prolonged gradually into a stem (cf. *Dendrocystis*).

Thecal plates clearly differentiated into: (*a*) smooth, irregular, and depressed interambulacrals; (*b*) transversely elongate adambulacrals. Diplopores at right angles to main food-groove, and confined to inner portions of adambulacrals. Each adambulacral bears a brachiole-facet; there are about thirty-six in each ray.

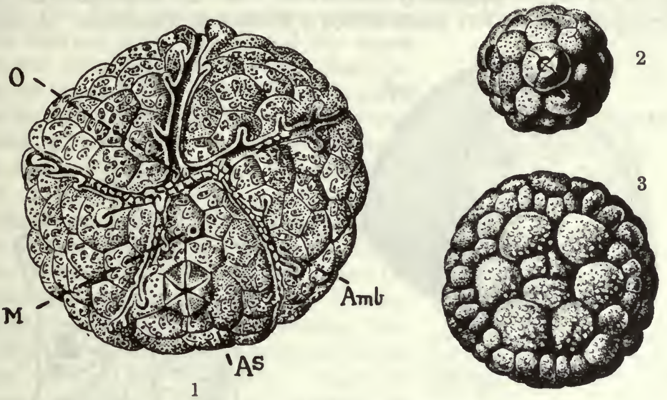


Fig. XLV.

Protocrinus oviformis, after Volborth. 1, oral surface, showing food-grooves partly covered by ambulacrals, $\times \frac{3}{2}$; 2, aboral surface of young individual, showing stem-attachment; 3, aboral surface of old individual, without stem.

Family 4. Mesocystidae. Diploporita in which the food-grooves extend over the theca almost to the aboral pole, and are regularly bordered by alternating brachioliferous adambulacrals, raised above and outside the adjacent interambulacrals. Diplopores confined to interambulacrals. Five interradial deltoids (Δ) surround the peristome. In this family we reach the final stage of the Diploporita, although a branch parallel with the Mesocystidae passes on in the direction of the Eublastoidea, beyond the boundary of the Cystidea. Genera—*Mesocystis*, Bather (Jan. 1898, = *Mesites*, Hoffmann, 1866; Nikitin, 1877; *Agelacrinus*, Schmidt, 1874), Ordovician, Esthonia. Theca (Fig. XLVII. 1) simulates that of a regular echinoid, or still more, *Edrioaster*, since the mouth is on the upper surface; from it narrow food-grooves, protected by covering-plates, pass straight down to the margin of the flattened aboral surface (Fig. XLVII. 2). Adambulacrals raised above the general surface of the theca, by the pushing in under them of the adjacent interambulacrals; thus they outwardly resemble the sub-ambulacrals or side-plates of Callocystinae (Fig. XLVII. 3). The interambulacrals do not, however, absolutely meet underneath the adambulacrals, but leave an irregular

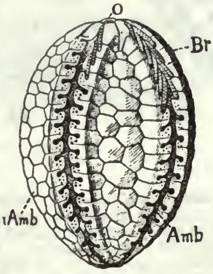


Fig. XLVI.

Proteroblastus, showing brachioles (*Br*), food-grooves (*Amb*) bordered by adambulacrals, and interambulacrals (*iAmb*). After Jaekel.

canal (which may have contained a nerve of the aboral nerve-system). Interambulacrals numerous and irregular, all pierced by diplopores. Mouth lies in a depression (cf. *Edrioaster*); surrounded by five interradial, slightly forked Δ, apparently continuous with the adambulacrals, and homologous with the five plates similarly situated in *Sphaeronis*. Posterior Δ pierced by hydropore (and ? gonopore). Anal pyramid in upper part of posterior interambulacrum. Aboral surface of theca composed of numerous small plates, but the structure of its central region is still unknown.

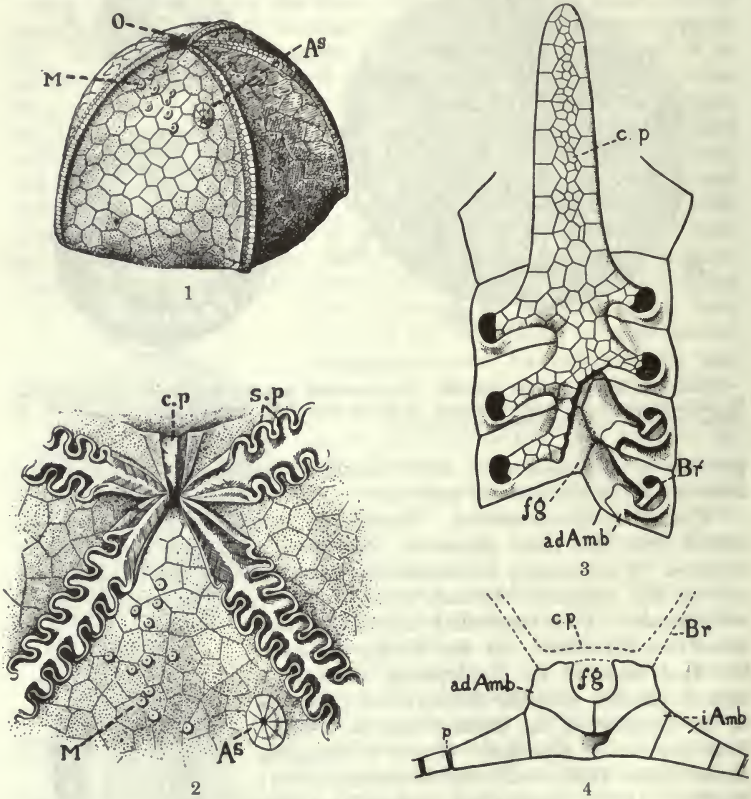


Fig. XLVII.

Mesocystis Pusirefskii. 1, general form, restored after Hoffmann and Nikitin. 2, oral surface, after Hoffmann, enlarged; the deltoids are not clearly shown. 3, structure of the adoral end of a food-groove, modified from Jaekel; the covering-plates removed from the lower right-hand part; much enlarged. 4, transverse section of a food-groove, after Jaekel. *As*, anus; *adAmb*, adambulacrals or side-plates (*s.p*); *cp*, covering-plates or ambulacrals; *Br*, dotted outlines of brachioles, borne by *Br'*, brachiole-facet; *fg*, food-groove; *iAmb*, interambulacrals, pierced by diplopores (*p*); *M*, supposed hydropores, probably only due to a boring parasite; *O*, mouth.

Family 5. Gomphocystidae. Diploporita in which extension of food-collecting surface is provided by the curving of the five main grooves around the theca and not by their prolongation on to brachioles.

Gomphocystis, Hall (1864), Silurian, N. America and Gotland (Fig. XLVIII.). Theca flattened above, greatly elongate below, composed of many irregular plates, pierced by diplopores. From a central mouth five food-grooves radiate over the theca, curving sinistrally around the upper part, and occasionally descending a short distance on the stem-like base. Covering-plates often strongly developed, and grooves lowered beneath thecal surface. Jaekel (1895) states that small side-grooves, but no brachioles, occur in a Gotland species. Anus close to mouth, in an interradius. Attachment appears to have been by the base, as in *Aristocystis*. The curving of the food-grooves and the asserted absence of brachioles cause *Gomphocystis* to resemble many Edrioasteroidea. But the structure of the grooves seems to be that which obtains in Diploporita, while the presence of marked diplopores confirms the reference to that order. In any case the family is out of the main line of evolution.

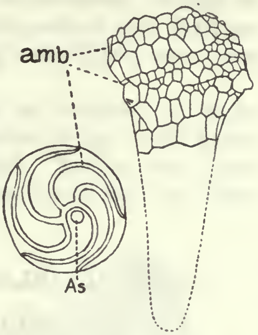


Fig. XLVIII.

Gomphocystis tenax, from above showing course of food-grooves, and from side with outlines of plates shown only in upper part. After Hall. $\times \frac{3}{2}$.

APPENDIX TO CYSTIDEA.

The following names have been supposed to refer to Cystids :—

Ascocystis, Barr., probably a Camerate Crinoid.

Balanocystis, Barr., indeterminable.

Camarocrinus, Hall (syn. *Lobolithus*, Barr.), root of a Crinoid (*Scyphocrinus*, *apud* Jaekel).

Cardiocystis, Barr., indeterminable.

Crinocystis, Hall, probably a Camerate Crinoid.

Cyclocrinus, Eichwald (*Pasceolus*, Billings), now regarded as calcareous Algae ; at any rate not Echinoderms.

Cystidea, a name used by Barrande for any indeterminable fragment, and not intended as a zoological genus.

Dictyocrinus, Conrad, is a Receptaculite.

Hyponome, Lovén, the ejected viscera and disc of an *Antedon*.

Hypocrinus, Beyrich, an Inadunate Crinoid (see p. 178).

Lichenocrinus, Hall, the root of a Pelmatozoan (see p. 133).

Mespilocystis, Barr., probably *Stephanocrinus* (see p. 96).

Neocystis, Barr., probably the root of a Pelmatozoan.

Porocrinus, an Inadunate Crinoid (see p. 172).

Rhombifera mira, Barr., is a *Stephanocrinus* (see p. 96).

A fairly complete **Bibliography** of the Cystidea was given in—

Barrande, J., 1887. Système Silurien du centre de la Bohème, 1re Partie : Recherches Paléontologiques. Vol. VII. Classe des Echinodermes. Ordre des Cystidées, 4to, xvii. and 232 pp., xxxix. pls. Prague.

The literature is so interwoven with that of Crinoidea and Blastoidea, that other references are reserved for the list at the end of Pelmatozoa (p. 211).

CHAPTER X.

THE BLASTOIDEA.[1]

CLASS II. BLASTOIDEA, Say (1825, *sensu extenso*).

GRADE A. **Protoblastoidea.**
„ B. **Eublastoidea.**

PELMATOZOA in which five (by atrophy four) epithecal ciliated grooves, lying on a lancet-shaped plate (? always), radiate from a central peristome between five interradial deltoid plates (Δ), and are edged by alternating side-plates bearing brachioles, to which side-branches pass from the grooves. Grooves and peristome protected by small plates, which can open over the grooves. The generative organs and coelom probably did not send extensions along the rays into the brachioles; but apparently nerves from the aboral centre, after passing through the thecal plates, met in a circumoral ring, from which branches passed into the plate under the main food-grooves, and thence supplied the brachioles. The thecal plates, however irregular in some species, always show defined basals (B) and a distinct plate ("radial," R) at the end of each ambulacrum; they are in all cases so far affected by pentamerous symmetry that their sutures never cross the ambulacra.[2]

The more primitive of these forms can hardly be distinguished from their immediate ancestors among the Cystids, such as *Proteroblastus* and *Mesocystis*, except by the more developed basals and radials; and it is this greater intimacy of correlation between ambulacral and thecal structures that necessitates their removal from the class Cystidea as here defined. Those general relations of the ambulacra to the theca, shared by Blastoidea with Diploporita, serve to distinguish them from the Callocystinae, with which some of the genera have been allied by naturalists. To these characters may be added the presence of diplopores, which are still to be found in the most primitive genus. From the

---

[1] By F. A. Bather, M.A.

[2] The term "ambulacrum" has been loosely used in the Blastoidea for the thecal elements connected with the food-groove. "Pseudambulacrum" is more correct and more cumbrous. The relations of the true ambulacral system are doubtful.

Edrioasteroidea they are separated by the presence of brachioles and absence of ambulacral pores. Their line of evolution, though in some respects parallel to those of the Callocystinae and Edrioasteroidea, was independently derived through the Diploporita from the primitive Amphoridea.

Within the class itself may be traced the increase of pentamerism, combined with a lessening in number of the thecal plates until a very definite arrangement is reached. At the same time, there is a concentration of semi-porous structures into the interambulacral region, and the evolution therefrom of elaborate respiratory organs (hydrospires); this is probably connected with the fact that all external connection with the water-ring (by means of a madreporite or hydropore) seems to have disappeared in the more specialised forms, and that, if the negative results of research may be trusted, there were no extensions of the water-vascular system into the brachioles.

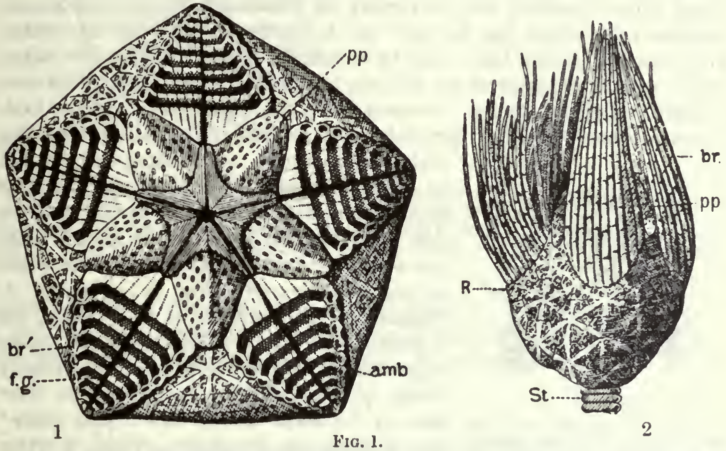


Fig. 1.

Asteroblastus. 1, oral surface of *A. stellatus;* not quite correct, as anal area is not shown. 2, side view of *A. Volborthi.* Both figures adapted from Schmidt, and × 2 diam. *amb*, so-called ambulacrum; *br*, brachioles, supported on *br′*, brachiole-facets; *f.g*, food-groove; *pp*, pore-plate, at adoral end of which is deltoid; *R*, radial, at end of ambulacrum; *St*, stem.

A somewhat arbitrary line may be drawn below forms that have acquired the normal definite number of plates and the hydrospire-folds hanging far into the thecal cavity; and while such forms constitute a grade Eublastoidea or Blastoidea *sensu stricto*, those below the line are Protoblastoidea.

GRADE A. **Protoblastoidea**, Bather (1899).

Blastoidea without interambulacral groups of hydrospire-folds hanging into the thecal cavity.

Family 1. Asteroblastidae. Protoblastoidea with an indefinite number of thecal plates, bearing diplopores, and with a pore-plate adjacent to, but distinct from, the deltoid in each interambulacrum. Genus—*Asteroblastus*, Eichwald (1862), emend. Schmidt (1874), Ordovician, Russia (Fig. I.). Theca pentagonal, on a relatively small round stem; its hemispherical dorsal portion is composed of 4 BB and 5 RR, between which are from twenty-five (*A. Volborthi*) to fifty (*A. stellatus*, type-sp.) polygonal plates; all plates have radiating ribs ("axial folds"), between which are diplopores. Round the mouth are 5 Δ, between which food-grooves pass to the ambulacra. Each ambulacrum consists of two rows of side-plates (adambulacrals), set alternately on either side of the food-groove, branches from which run to right and left between adjacent side-plates. Any underlying plate there may be is entirely covered by the side-plates. At the ends of the grooves are sockets, by which uniserial brachioles were attached to the side-plates. Grooves down the brachioles joined the food-grooves of the ray, and all probably were covered with small alternating plates (ambulacrals). Adjoining each Δ and separating the adjacent ambulacra, is a large diplopore-bearing plate; in *A. tuberculatus* this is much like other plates of the theca (on which ground Haeckel has separated the species as *Asterocystis*, Fig. II.); but in *A. stellatus* and *A. Volborthi* it is enlarged, has a pronounced median crest, and is almost separated by the ambulacra from the ordinary thecal plates. [The anus appears to have been at the distal end of this "pore plate" in one of the interambulacra, which is wider than the others.] Family 2. Blastoidocrinidae. Protoblastoidea with a definite number of thecal plates, without diplopores, and without distinct pore-plate. Genus—*Blastoidocrinus*, E. Billings (1859), Canadian, and Schmidt (1874), Russian, Ordovician, is only known from imperfect specimens, so that only the following details can be given (Fig. III.):—The small round stem is inserted into a considerably invaginated base, as is the case in several crinoids. BB, at least 3. RR, 5, not notched for reception of ambulacra, but with truncate upper margin; they support 5 large interradially situate Δ. Each Δ consists of two parts: an orad, subtriangular piece, like that called deltoid in *Asteroblastus*, and a lower, triangular piece corresponding to the pore-plate in *Asteroblastus*; the connection between the two parts is still slight; indeed, in Canada the orad portions are often fused with one another into a pentagonal frame. The lower portions show a marked striation, due to stroma strands, at right angles to the radio-deltoid suture, and on the sutural edge the stereom is thrown into folds (incipient "hydrospires") which, however, have not been observed to pass into the RR. The food-grooves pass out between the Δ; the lancet-plate supporting them is covered by alternating side-plates, which receive branches from the main groove, and are provided with a clear brachiole-facet; the remains of brachioles are

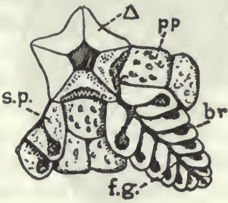
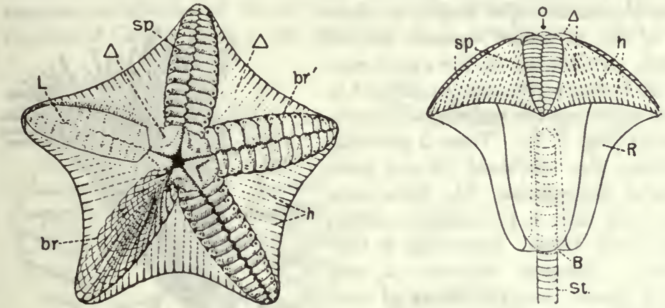


Fig. II.

Portion of the oral surface of *Asteroblastus (Asterocystis) tuberculatus*. Δ, the five deltoids surrounding the peristome; *s.p*, side-plates or adambulacrals. Other letters as in Fig. I. (After Schmidt.) ×2 diam.

preserved, as in *Asteroblastus* and many Eublastoids. These known facts afford no character, other than the less development of the hydrospires, by which *Blastoidocrinus* should be separated from the Eublastoidea, so long as that order includes such a form as *Codaster*. But till the structure of the base and the position of the anus are known, the genus may be kept with its rather more primitive allies, *Asteroblastus* and *Asterocystis*.



1 FIG. III. 2

Blastoidocrinus carchariaedens; restored on the evidence of E. Billings. 1, oral surface; 3 rays show the side-plates (*sp*) with their facets for brachioles (*br′*); 1 ray shows the brachioles (*br*) attached; the 5th ray shows lancet-plate (*L*) exposed by removal of side-plates. 2, from the side; the upward extension of the stem (*St*) and the invaginated basals (*B*) are indicated by dotted lines. *h*, incipient hydrospires.

GRADE B. **Eublastoidea**, Bather (1899).

(=BLASTOIDEA, *Auctt.*).

Blastoidea in which the thecal plates have assumed a definite number and position in three circlets, as follows:—3 BB, 2 large (formed by fusion of two pairs of the primitive 5 BB) and 1 small, in r. ant. IR; 5 RR, often fork-shaped, forming a closed circlet; 5 Δ, interradial in position, supported on the shoulders or the processes of the RR, and often surrounding the peristome with their oral ends. The stereom of the RR and Δ on either side of the ambulacra is thrown into folds running across the radio-deltoid suture; these folds hang down into the thecal cavity, forming the hydrospires.

Beginning in the Silurian with *Codaster* and *Troostocrinus*, we may trace the gradual modification of a simple type, and the evolution of the numerous complicated structures characteristic of so specialised a form as *Pentremites*. Starting afresh with *Elaeacrinus* we shall study the elaboration of the structures that characterise *Orbitremites* (=*Granatocrinus*), which represents the acme of the Eublastoidea in Britain. Thus the morphology and the classification will be unfolded along with the phylogeny.

Codaster, M'Coy (1849), Silurian to Carboniferous, Britain and N. America, is the least specialised of all Eublastoids (Fig. V.). The 3 BB form a conical cup, on which follows the more cylindrical circlet of 5 RR, the processes of which bend in above almost at right angles, to form part of the truncated summit or oral surface. Following on the upper margins of the radial processes come the 5 Δ, which surround the pentagonal mouth-opening (Fig. V. 1). These Δ probably represent the combined Δ and pore-plates of *Asteroblastus;* like those pore-plates they have a pronounced median crest ("oral ridge," Etheridge & Carpenter). Between adjacent Δ, and passing down into the sinus of each R, is a long plate, known from its shape as the "lancet-plate" (Fig. V. 2); the edges of this partly overlap the R and Δ; its upper surface bears a groove which passes between the adjacent Δ to the mouth. It is pierced by a central canal, comparable to the central hollow seen in *Mesocystis*, and probably filled by a nerve from the aboral system (Fig. V. 6). Along the sides of the lancet-plate lie small "side-plates," not, however, in single series, but in zigzag, so that each pair forms a rhombohedron bisected by the suture between them (Fig. VI.). On these sutures are brachiole-facets; and branches from the ventral groove pass alternately to the side-plates, and on to the brachioles. The whole groove was covered by small movable plates, the impressions of which are seen along its sides. The peristome was similarly plated over. The apposed edges of the radial processes and the Δ are thrown into a set of strongly-marked folds at right angles to the radio-deltoid sutures (Fig. V. 6). These folds in the stereom may be an exaggeration of the axial folds so conspicuous in *Asteroblastus;* the stereom forms a thin-folded wall, the ends of the folds dipping far down into the thecal cavity. One infers from similar foldings in other animals

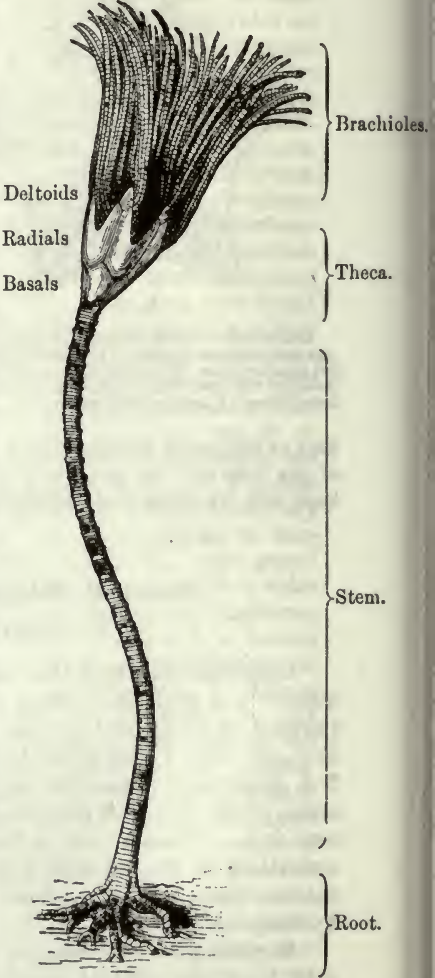


Fig. IV.

Reconstruction of a typical Eublastoid, *Orophocrinus* (vel *Dimorphicrinus*) *fusiformis*, from Kinderhook beds of Iowa. By permission of the Keeper of the Geological Department of the British Museum.

that the object was an increase of surface for respiratory purposes, the outer oxygenated sea-water passing down into the folds and the inner coelomic fluid passing up into the alternate folds. Hence to such structures E. Billings gave the name "hydrospires." They are similar, in essential structure and in position across the suture lines, to the pectinirhombs of Callocystinae; and similarly are a development of the normal structure of the test. The marked pentamerous symmetry of the thecal plates (with the apparent exception of BB) and of the hydrospires is disturbed only by the anus, which makes an opening between the posterior Δ and the adjacent radial processes. From this IR hydrospire-folds are said to be absent (but one or two may be seen in some specimens, Fig. V. 2). The anal opening was closed by small plates. The essential structures of *Codaster* are all to be found in Protoblastoidea; the absence of interambulacrals, in *Blastoidocrinus;* the ambulacral structures, in

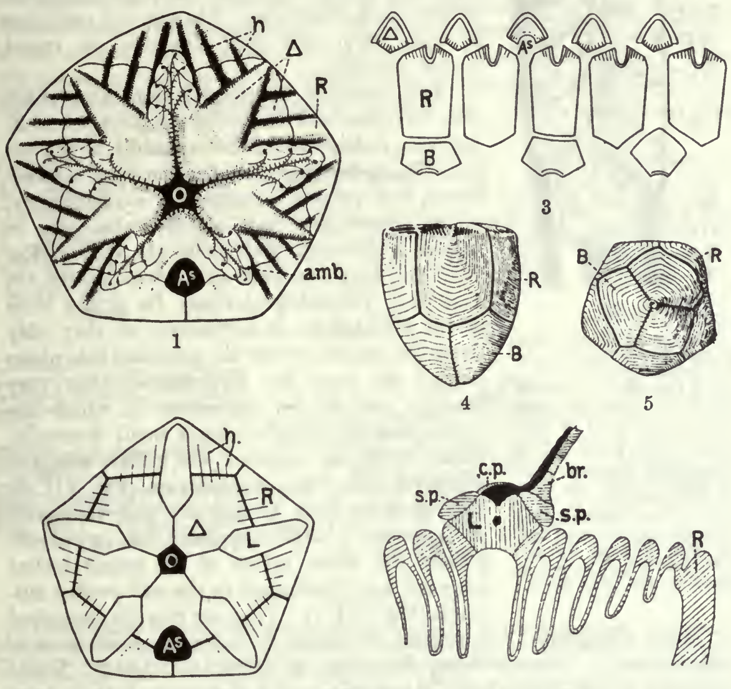


Fig. V.

Codaster trilobatus. 1, oral surface of young individual of var. *acutus*, with 3 hydrospires each side of a food-groove and traces of them in anal interradius (Brit. Mus. E8020). 2, a theca ground down from the oral surface, thus bringing out the sutures (Brit. Mus. E8023). 3, analysis of the main thecal elements. 4, theca seen from the left posterior radius. 5, the same theca from below, with posterior interradius uppermost. (Both from Brit. Mus. E8013). × $\frac{3}{2}$. 6, slightly restored section across part of a radius. *amb*, so-called ambulacrum or pseudambulacrum, with food-groove; *As*, aperture for anus; *B*, basal; *br*, brachiole; *c.p*, covering-plates; *h*, hydrospire-folds; *L*, lancet-plate; *O*, mouth-aperture; *R*, radial; *s.p*, side-plate; Δ, deltoid.

Asteroblastus and *Blastoidocrinus* ; the position of the anus, in *Asteroblastus*; the hydrospires, though far less developed, in *Blastoidocrinus*. So much is this the case that *Codaster* has been referred to the Cystidea by several writers of eminence. Further arguments for such action are found in the fact that *Codaster* has no "spiracles" at the proximal ends of the ambulacra, and no hydrospire-pores along their sides, structures which are often considered characteristic of the Eublastoidea. The gradual evolution of these structures may, however, be traced within the order.

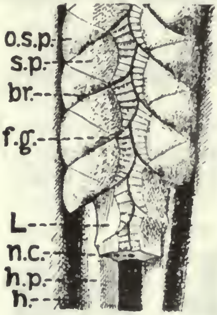


FIG. VI.

Food-groove and associated structures of *Codaster trilobatus*, greatly enlarged. *o.s.p*, outer side-plate; *s.p*, side-plate; *br*, brachiole-facet, from which passes a small groove to *f.g*, the main food-groove, along which are impressions of covering-plates. These structures are borne by *L*, lancet-plate, in which is *n.c*, a possible nerve-canal. Beneath this emerges *h.p*, the plate forming the side of *h*, the first hydrospire-fold. (Based on Brit. Mus. E8027.)

Phaenoschisma, Etheridge & Carpenter (1882, -86), Devonian and Carboniferous, Europe and N. America, differs from *Codaster* mainly in the fact that the hydrospire-folds become more concentrated, and pushed in under, or overgrown by, the side-plates and part of the lancet-plate, so that as a rule only their ends are visible (Fig. VII. 2); they are also well developed in the anal IR. The side-plates may lie at the sides of the lancet-plate, as in *Codaster*, or they may lie on it ; in cases where the proximal side-plates project far over the hydrospires, they may entirely roof in the depression in which the hydrospires lie, only leaving a small communication with the exterior on either side the proximal end of the ambulacrum (Fig. VII. 6). The openings thus formed are the rudiments of "spiracles." The side-plates that in *Codaster* formed the outer halves of the rhombohedral pairs are here diminished in size and pushed outwards (Fig. VII. 1). They are now distinguished as "outer side-plates" (cf. similar structures in the recumbent arms of Callocystinae). *Cryptoschisma*, Etheridge & Carpenter (1886), Lower Devonian, Spain, differs from *Phaenoschisma* and *Codaster* in little but the greater breadth of the ambulacra, which entirely conceal the eight hydrospire-slits on either side. Sometimes the ambulacra do not reach to the tops of the deltoid crests (or oral ridges), and thus there is a spiracle on either side of each crest, or ten in all ; but sometimes they reach right up the oral ridges, so that the spiracles of adjacent ambulacra become confluent, and there are five in all (Fig. VII. 8). This is expressed by saying spiracles "double" or "single" respectively. *Orophocrinus*, von Seebach (1864 ; synn. *Dimorphicrinus*, d'Orb. ; *Codonites*, Meek & Worth), Carboniferous, Britain, Belgium, and N. America (Fig. IV.). The hydrospire-slits are more concentrated at the bottom of the depression for the ambulacra ("radial sinus") than in previous genera ; but since the ambulacra are narrower, some of the slits may be exposed, and the spiracles are merely clefts, often extending all along the sides of the ambulacra (Fig. VII. 7). The concentration of the hydrospire-slits causes the inner walls of the two nearest the median line of the ambulacrum to meet along that line, and so to form a new structure known as the "under lancet-plate" ("sub-lancet"). In this genus the oral surface is raised into more or less of a dome, so that the Δ are visible in side view. Post. Δ encloses the anus.

Pentremitidea, d'Orbigny (1849, emend. Eth. & Carp., 1882,-86), Devonian, Spain, the Eifel, and N. America. In the form of the calyx, the complexity of the hydrospires, and other points there is great variability. *P. Paillettei*, de Vern., however, type of the genus, is not far removed from *Phaenoschisma* and *Cryptoschisma*. Eight hydrospire-folds lie on each side of an ambulacrum, entirely covered by the broad lancet-plate. The side-plates are on top of the lancet-plate, so that none of it is visible. The outer side-plates are wedged in between the side-plates and do not project beyond their edges. Δ covered by radial processes, so that only the crests are exposed. The spiracles are clefts on either side the ambulacra, between the deltoid crests and the proximal side-plates. The anus pierces post. Δ, which therefore has no crest, so that the adjacent spiracles are confluent with the anus; the opening so formed is called "the anal spiracle." In some species (esp. *P. angulata*) the side-plates do not cover the lancet-plate any more than they do in some species of *Phaenoschisma*. Within the limits of *Pentremitidea* (as defined by Etheridge & Carpenter) two changes of importance take place. The hydrospires no longer remain extended, with each fold opening into the space below the

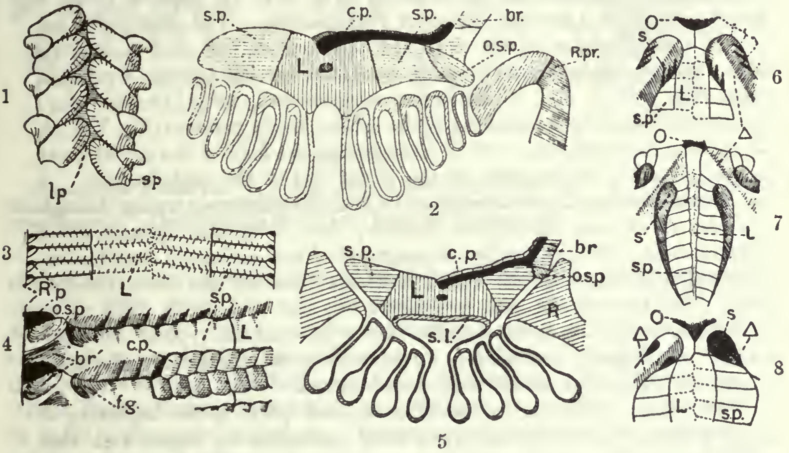


Fig. VII.

1, *Phaenoschisma Verneuili*, food-groove seen from above. *lp*, lancet-plate; *sp*, side-plates, between which are the small outer side-plates. 2, section across part of a radius of the same; the hydrospires are here in the deltoid, and only a process of the radial is seen (*R.pr*). 3, part of an ambulacrum of *Pentremites*, seen from above, × 6 diam. 4, left side of the same further enlarged, showing some of the covering-plates (diagrammatised from Steinmann). 5, section across a radius of *Pentremites*, × 6 diam. 6-8 are diagrams showing the evolution of spiracles: 6, in *Phaenoschisma*; ends of hydrospire-folds still visible, only an incipient spiracle. 7, in *Orophocrinus*; a long spiracle-slit is enclosed between side-plates and deltoid ridge. 8, in *Cryptoschisma*; on the left the spiracles are distinctly separated by the deltoid ridge; on the right the side-plates of adjacent ambulacra meet and the deltoids sink, so that the spiracles appear single. *br*, brachiole; *br'*, articular facet for same; *c.p*, covering-plates; Δ, deltoid crest; *f.g*, food-groove; *L*, lancet-plate; *O*, peristome; *o.s.p*, outer side-plate; *p*, pores; *R*, radial; *s*, spiracle; *s.l*, sub-lancet; *s.p*, side-plate.

overspreading ambulacrum, but the admedian folds become gradually lowered into the thecal cavity and open into a common canal (e.g. *P. clavata*); thus each system of folds forms a "pendent" hydrospire-sac. The second change is the slight notching or bevelling of the ends of the side-plates and the projection of the outer side-plates so as to touch the wall of the radial sinus; thus is formed along each side of the ambulacrum a series of openings by which water is admitted to the hydrospires, which it bathes and then passes out again by the spiracles (e.g. *P. lusitanica*); these openings are called "pores," but are not comparable to the haplopores or diplopores of the Cystidea, to the water-pores of Crinoidea, or to the ambulacral pores of Echinoidea. *Pentremites*, Say (1820, originally *Pentremite*), Carboniferous, N. America (Fig. XV. 1), appears to be a descendant of the American species of *Pentremitidea*. The chief difference is that the side-plates do not cover the lancet-plate, but rest against its edge; thus the ambulacrum becomes much broader and assumes a petaloid shape (Fig. VII. 3, 4). A sub-lancet is developed, as in *Orophocrinus;* hydrospire-folds 3 to 9 according to the species, freely pendent (Fig. VII. 5), as in some *Pentremitidea ;* but in some species the floor of the radial sinus meets below the hydrospires at the distal end of the ambulacrum. A canal runs between the hydrospires and the side-plates, emerging through spiracles which may be single or double; there is an anal spiracle, as in *Pentremitidea*. Though limited in geographical and geological distribution, *Pentremites* has more species and individuals than has any other Blastoid genus; for this reason, and because it was the first of its class to be introduced to science, it has usually been treated as the type of the Blastoidea. Zoologically considered, however, it merely represents the acme of one particular line which thereafter died out.

We return, therefore, to the Silurian, and take up the beginning of another line of development, apparently connected in origin with that which has just been traced and not very divergent therefrom.

Troostocrinus, Shumard (1866, emend. Eth. & Carp., 1886), Silurian, N. America, might be expected from its geological position to be a primitive form; and that it is such is shown by the structure of the ambulacra (Fig. VIII.). The chief differentiation from the *Codaster* type lies in the elevation of the radial processes; the restriction of all Δ, except post. Δ, to a very small truncate summit, so that the hydrospire-folds are almost entirely formed out of the radial stereom; the narrowing of the radial sinus, so that (as in some species of *Phaenoschisma*) the side-plates are pushed up on to the top of the lancet-plate, while the hydrospire-folds are pushed beneath it. The outer side-plates are small, subtriangular, squeezed out to the edge of the side-plates, with which they alternate; they touch the wall of the radial sinus so that "pores" are formed between them. The hydrospire-folds are midway between the Codasterid type and the pendent type; their admedian walls, which support the lancet-plate, are thickened, and tend to form "hydrospire plates," covering the immediately adjacent folds. The canal that runs along above the hydrospires and below the lancet and outer side-plates comes to the surface at the oral end through a spiracle bounded by the Δ and lancet-plate, and since the deltoid crests are slight, the spiracles are almost single. The anus opens through the posterior spiracle, *i.e.* through the oral end of post. Δ; the position is less primitive than in *Codaster*, but the greater size of post. Δ seems primitive. *Metablastus*, Eth. & Carp. (1886), is represented by doubtful species in the Silurian of N. America, less doubtful from Devonian of Europe, and undoubted from Lower Carboniferous of N. America. It closely resembles *Troostocrinus* in form; but the Δ are all equal, small, and confined to the summit, while the two posterior spiracles are distinct from the anus. In structure the ambulacra scarcely differ from those of *Troostocrinus;* but the lancet-plate of *M. lineatus* is said to have three longitudinal canals •.•, the meaning of which is not obvious (cf. *Schizoblastus*). The base is elongate, and triangular in section, with flattened sides. *Tricoelocrinus*, Meek & Worthen (1868), Carboniferous, N. America, and (?) Queensland (Fig. XV. 2), owes its name to three excavations along the interbasal sutures, corresponding to the three flattened sides of *Metablastus.* A feature of more importance is the enclosure of the distal portion of the hydrospires within the thickness of the radial plate; this is probably due to the upward growth of the floor of the sinus, as has taken place, independently and to a less extent, in *Pentremites. Eleutherocrinus*, Shumard & Yandell (1856), Devonian, N. America, is probably a descendant of *Troostocrinus.* It has, however, lost its stem and adopted some mode of life that has affected its symmetry. The place of the stem is occupied by the small r. ant. B. The two other BB are pushed a little to the side and produced up the theca to meet the broadened and shortened l. post. R. The remaining RR, with their ambulacra, are much like those of *Troostocrinus* and *Metablastus;* this l. post. R, however, bears a short ambulacrum with only seven side-plates on either side, but these greatly widened transversely to the median groove, and curved distalwards (Fig. IX.). There are small Δ, and (*apud* Shumard) spiracles at their oral ends on either side of each normal ambulacrum. The anus is stated by Wachsmuth (in Whiteaves, 1889) to lie on the right upper margin of the abnormal R, and therefore at the aboral end of the Δ. Sections across the ambulacra (Eth. & Carp., 1886) show a lancet-plate with large longitudinal canal, and seven hydrospire-folds, arranged as in *Troostocrinus*, on either side of each ambulacrum in its

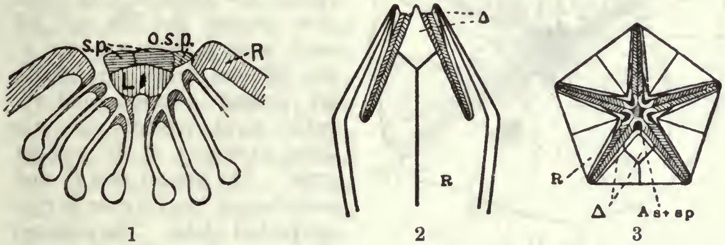


FIG. VIII.

Troostocrinus Reinwardti. 1, section across a radius, much enlarged. 2, upper part of theca, posterior view. 3, oral surface of theca. Lettering as before. *As+sp*, anus and confluent spiracles. (2 and 3 slightly altered from Etheridge & Carpenter.)

upper part; at the aboral end of the ambulacrum the floor of the radial sinus comes below the lancet-plate (cf. *Tricoelocrinus*).

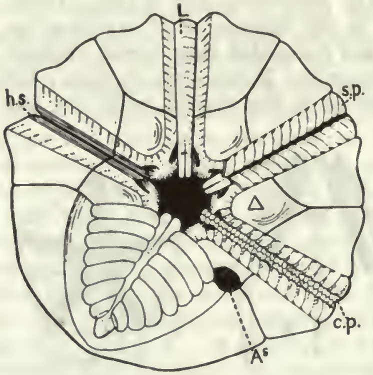
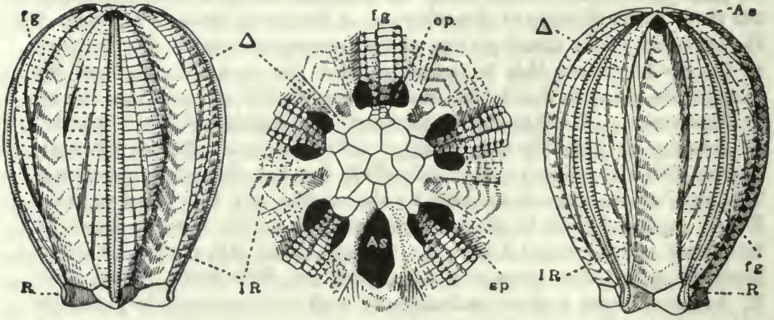


Fig. IX.

Eleutherocrinus Cassedayi; oral view × 6 diam. The abnormal, l. post. radius turned to the observer; r. post. ray has covering-plates (*c.p*) which in life would have covered over the oral centre; in r. ant. ray the *c.p* are removed and one sees the whole of the side-plates (*s.p*); these again are removed from ant. ray, exposing the lancet-plate (*L*); removal of *L* in l. ant. ray shows the hydrospires (*h.s*). (Based on Shumard & Yandell, and Whiteaves.)

Nucleocrinus, Conrad (1842, synn. *Elaeacrinus*, Roemer, 1851; and *Olivanites*, Troost, MS., 1849), Devonian, North America, differs much from the genera hitherto described (Fig. X.). Although the theca is lofty (often olive-shaped) the BB and RR reach a very short way up it; the BB and lower part of RR are pressed inwards, and the radial sinus receives only the distal extremity of the ambulacrum. The greater part of each ambulacrum lies between certain interradial plates. The posterior interradius contains three such plates—a median plate, at the oral end of which lies the anus, and a plate on either side. These lateral pieces meet at their oral ends, enclosing the anus, and stretch down between the central piece and the ambulacra. The central interradial is smooth, with a median vertical ridge; but the lateral pieces are transversely grooved, each groove corresponding to a pore in the ambulacrum. As regards the structure of the other interambulacra there is a difference of opinion. Each contains a lanceo-



1 2 3

Fig. X.

Nucleocrinus Verneuili. 1, from anterior radius, × $\frac{3}{2}$. 2, oral view, showing large covering-plates over the peristome (from Brit. Mus. E20), × $\frac{3}{2}$. 3, from posterior interradius, × $\frac{3}{2}$. *As*, anus; *cp*, covering-plates, which were continuous over the food-groove (*fg*); *IR*, interradial pieces; *R*, radials; *sp*, spiracles; Δ, deltoids, the limbs of which flank the ambulacra.

late central area, with a median ridge, separated from the ambulacra by transversely grooved areas meeting adorally. Some specimens show appearances of sutures between these areas, especially at the aboral end. Hence Lyon (1857), from the study of many hundred specimens, and Billings (1870) concluded that these interambulacra also contained three plates, as a rule fused together. Roemer and Etheridge & Carpenter, however, believed that there was only one plate, and that the markings were merely ornament. The ambulacra are narrow; their structure is shown in Figs. X. 2 and XI. They dip down to the mouth underneath a roof of strong plates. The hydrospires are pendent, their folds reduced to two; they emerge through large spiracles, separated by the interambulacral plates. As for the homologies of the thecal plates, those who believe that there is only one in each interambulacrum regard that one as the Δ, which in the posterior interradius is split in two by an intercalated anal plate. This makes *Nucleocrinus* a highly specialised form, into which is suddenly introduced an element found in no other Eublastoid. If, however, we accept the view that each interambulacrum has essentially the same composition, viz. three plates, we are able to institute comparisons with Protoblastoidea. These suggest that the true homologues of the Δ in *Nucleocrinus* are the proximal portions only of the plates called deltoid by Etheridge & Carpenter. This latter explanation of the structure of *Nucleocrinus* permits us to regard it as primitive in all except the hydrospires, and consists better with its geological age. *Schizoblastus*, Eth. & Carp. (1882-86), Carboniferous, Britain and N. America, may be described as a *Nucleocrinus* in which there is only one plate in each of the interambulacra; this therefore may be called a deltoid, but may well represent the three plates some suppose to exist in *Nucleocrinus*, since it preserves their peculiar sculpturing. In some species it is of much less relative size. The hydrospires, as in *Nucleocrinus*, are of simple structure, with one to four folds. In two American species the posterior spiracles are separate from the anus, as in *Nucleocrinus;* in others they are confluent. The plates roofing the mouth, though not quite so stout as in *Nucleocrinus*, are usually well preserved. *Cryptoblastus*, Eth. & Carp. (1886), Carboniferous, N. America, is like a *Schizoblastus* with small Δ. The hydrospires differ from those of *Nucleocrinus* and *Schizoblastus* only in the development of hydrospire-plates (cf. *Troostocrinus*) which extend right up the sides of the lancet-plate, separating it from the folds and from the walls of the radial sinus. But where the Δ are

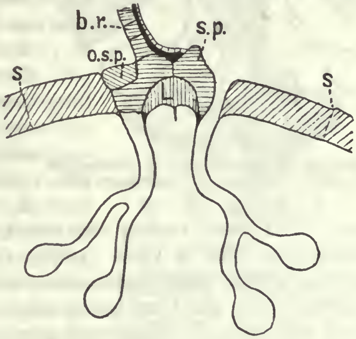


FIG. XI.

Section of ambulacrum of *Nucleocrinus Verneuili*, × 10 diam. *b.r*, brachiole; *L*, lancet-plate; *o.s.p*, outer side-plate; *s.p*, side-plate; *s*, supposed suture between lateral and central interambulacrals.

reached, the lancet-plates abut directly on them, without leaving any pores; the hydrospire-canals pass up beneath the lancet-plates, and open through spiracles on either side of each Δ. *Orbitremites*, T. & T. Austin (1842, generally known as *Granatocrinus*, Hall, 1862), Carboniferous, England, N. America, and (?) Queensland (Fig. XV. 3, 4). The general shape and relations of the plates are as in *Schizoblastus* and *Cryptoblastus.* Hydrospires the same as in *Cryptoblastus* (Fig. XII.). The hydrospire-canals here are surrounded by the Δ, and pass through them to five single spiracles (the posterior confluent with the anus) at the apices of the Δ, which sometimes project as short tubes. The plates roofing the mouth are minute and usually irregular. *Heteroblastus*, Eth. & Carp. (1886), Carboniferous, England, and (?) N. America, differs from *Orbitremites* in that the hydrospire-canals pass beneath the Δ, and then curve outwards on either side of each Δ. The adoral end of the Δ is produced upwards as a short stout process. *Mesoblastus*, Eth. & Carp. (1886), Carboniferous, England, Belgium, (?) N. America and Queensland, differs from *Orbitremites* in that the hydrospire-canals are continued upwards over the flattened lateral portions of the Δ, and open at the sides of the Δ crest. . In some species the crest is almost absent, and the spiracles therefore almost single. *Acentrotremites*, Eth. & Carp. (1883-86), Carboniferous, Somerset, is only known from one specimen, but is a far more distinct genus than those just described (Fig. XIII.). The general form is that of *Orbitremites.* The hydrospires do not pass up into the Δ, but the canal opens immediately on the suture between Δ and R; there are thus ten spiracles, as in *Schizoblastus Sayi.* The anus pierces post. Δ, close to its adoral end. The number of hydrospire-folds is unknown; the inner walls form a structure meeting in the median line, and thus like a sub-lancet; but also passing up the sides of the lancet-plate, and thus like a hydrospire-plate. The lancet-plate is small and perforate; it is covered by small side-plates and large outer side-plates.

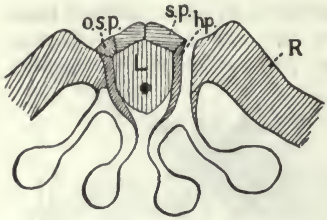


FIG. XII.

Section of ambulacrum of *Orbitremites Norwoodi*, ×10 diam. *hp*, hydrospire-plate.

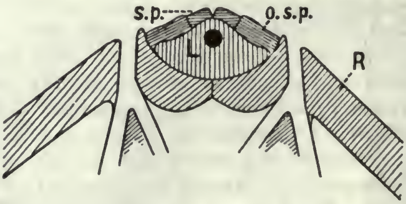


FIG. XIII.

Transverse section of ambulacrum of *Acentrotremites ellipticus.*

Pentephyllum, Haughton (1859), Carboniferous, Limerick, is based on a single internal cast. It is said to be unstalked, and this condition, if obtaining, is correlated with the asymmetry shown in the slight shortening of one ambulacrum and the slight curve of the adjacent ambulacra towards the opposite side. The linear ambulacra, the large Δ, and the strictly pentagonal base remove it from the other irregular Blastoids, and suggest affinities with the group of genera last discussed. *Zygocrinus*, Bronn (1848, syn. *Astrocrinus*, T. & T. Austin, 1843, *non* Conrad, 1840, *nec Asterocrinus*, Münster), Carboniferous, Britain (Fig. XIV.). This highly asymmetrical form has been elaborately described by R. Etheridge, fil. (1876), and by Etheridge & Carpenter (1886), but its affinities remain uncertain. Its resemblance to *Eleutherocrinus* lies only in secondary characters induced by a sessile life. The theca is depressed, stemless, and produced into four lobes; on the shortest of these lies an ambulacrum modified much as in *Eleutherocrinus*, and towards it the two larger BB stretch up as in that genus. The four normal ambulacra lie in the depressions between the lobes. Three Δ are large and stretch out over the lobes; two are small and flank the abnormal ambulacrum. Anus and spiracles unknown. One hydrospire-fold lies on each side of the radial sinus, and is enclosed by it at the distal end (cf. *Pentremites*, *Tricoelocrinus*). The surface is covered with strong tubercles which bear minute spines (cf. *Hystricrinus* = *Arthracantha*, p. 158).

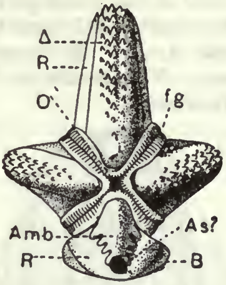


FIG. XIV.

Zygocrinus Benniei, after Etheridge & Carpenter, × 10 diam. Oral view, modified food-groove (*Amb*) towards the observer; *O*, peristome; *As?*, a doubtful opening. Other letters as usual.

Classification.—We have now reviewed every known genus of Eublastoidea, in an order approximating, as near as our very imperfect knowledge of many types will allow, to that of their race-history. This seems to show three main branches: one leading from *Codaster*, through *Phaenoschisma*, to *Pentremitidea* and *Pentremites*, with offshoots *Cryptoschisma* and *Orophocrinus;* the second from *Troostocrinus*, through *Metablastus*, to *Tricoelocrinus*, with the offshoot *Eleutherocrinus;* the third from *Nucleocrinus*, through *Schizoblastus*, to *Cryptoblastus*, *Orbitremites*, *Mesoblastus*, and *Heteroblastus*, with an offshoot *Acentrotremites*, and probably *Pentephyllum*. *Zygocrinus* also is perhaps connected with this third line of descent.

The classification of Etheridge & Carpenter does not agree very well with the phylogeny here outlined. The erection of an "Order Irregulares" is no more likely to be correct for Blastoidea than for Crinoidea. With the exception of the Codasteridae, their families of the "Regulares" are based almost entirely on the relations of the hydrospire canals to the deltoids, relations which may vary considerably even in an individual, while they take no account of important differences in the relations of the hydrospires to the ambulacra. Moreover, in the construction of family names, these authors have contravened the laws of nomenclature.

The following classification attempts to overcome the above objections while making as little change as possible:—

Series A. CODONOBLASTIDA. FAMILY 1. CODASTERIDAE. Hydrospire-folds distinctly portions of the thecal plates, coming to the surface of the radial sinus. No distinct hydrospire-canal or pores; spiracles developed imperfectly or not at all. Genera—*Codaster*, *Phaenoschisma*, *Cryptoschisma*, *Orophocrinus*. This family coincides with that of Etheridge & Carpenter. Family 2. Pentremitidae. Hydrospire-folds, usually numerous, concentrated at the lowest part of the radial sinus, and partly or wholly pendent. Hydrospire-canal opens through spiracles bounded distally by side-plates. Base convex. Ambulacra rather broad. Genera—*Pentremitidea*, *Pentremites*. This equals the *Pentremitidae* of Etheridge & Carpenter, *minus Mesoblastus*.

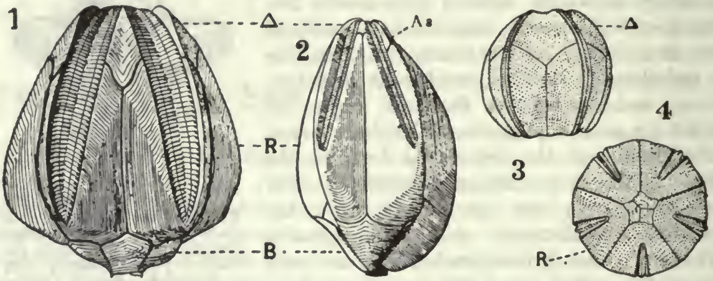


Fig. XV.

Thecas of typical Blastoids. 1, a Codonoblastid—*Pentremites robustus* (from Brit. Mus. E8145). 2, a Troostoblastid—*Tricoelocrinus woodmani* (from Brit. Mus. E8171). 3 and 4, a Granatoblastid—*Orbitremites orbicularis* (from the type-specimens, Brit. Mus. E8135). 3, from the side. 4, from below, with posterior interradius uppermost. All figures nat. size.

Series B. Troostoblastida. Family 1. Troostocrinidae. Elongate forms with linear ambulacra descending sharply outwards from the much restricted peristome. Hydrospire-folds only slightly concentrated, but communicate with exterior through pores, and through spiracles bounded by Δ and lancet-plates. Genera—*Troostocrinus*, *Metablastus*, *Tricoelocrinus*. This equals the *Troostoblastidae* of Etheridge & Carpenter. Family 2. Eleutherocrinidae. Elongate, stemless, asymmetrical, with four narrow ambulacra, accompanied by unconcentrated hydrospires. Fifth ambulacrum shortened and widened. Δ minute. Genus—*Eleutherocrinus*.

Series C. Granatoblastida. Family 1. Nucleocrinidae. Interambulacra show traces of a primitive triad of plates. Ambulacra linear, and stretching far down the theca, which is ovoid. Hydrospire-folds few and pendent. Spiracles double. Mouth roofed by large plates firmly united into a tegmen. Genera—*Nucleocrinus*, *Schizoblastus*. This family equals Etheridge & Carpenter's Nucleoblastidae, *minus Cryptoblastus* and *Acentrotremites*. Family 2. Orbitremitidae. Theca globular with concave or flattened base. Ambulacra linear, stretching down to concavity of base. Hydrospire-folds few and pendent; a hydrospire-plate always present (unknown in *Heteroblastus*). Hydrospire-folds rarely penetrate Δ, but long canals pass onward, through, beside, or under them, except in *Acentrotremites*. Genera—*Orbitremites*, *Cryptoblastus*, *Heteroblastus*, *Mesoblastus*, *Acentrotremites*. This corresponds to Etheridge & Carpenter's Granatoblastidae, *plus Cryptoblastus*, *Mesoblastus*, and *Acentrotremites*. Family 3.

PENTEPHYLLIDAE. Theca subpentagonal, stemless; RR asymmetrical. Ambulacra linear, stretching down to base. One shorter than the rest. Genus—*Pentephyllum.* FAMILY 4. ZYGOCRINIDAE. Theca depressed, stemless, asymmetrical, quadrilobate. Four ambulacra between the lobes, accompanied by a single hydrospire on either side. Fifth ambulacrum shortened and widened. Δ large. Genus—*Zygocrinus.*

A **Bibliography** of the Eublastoidea was given by R. Etheridge, jun., and P. H. Carpenter, "Catalogue of the Blastoidea in the . . . British Museum," London, 1886. A complete index of names with references to literature is furnished by F. A. Bather, "The Genera and Species of Blastoidea, with a List of the Specimens in the British Museum," London, 1899. For other references see Nos. 16, 17, 25, 27, 30, 34, 38, 45, 50, 60, 64, 69, 71, 73, 75, 76, 77, 78, 82, 84, 85, 94, 95, 96, in the list at the end of Pelmatozoa (p. 211).

CHAPTER XI.

THE CRINOIDEA.[1]

CLASS III. CRINOIDEA, MILLER (1821)

(=CRINOIDEA BRACHIATA, *Auctt. veterum;* EUCRINOIDEA, Zittel, 1879).

SUB-CLASS 1. MONOCYCLICA.

- Order 1. **Inadunata.**
- ,, 2. **Adunata.**
- ,, 3. **Camerata.**
  - Sub-Order 1. **Melocrinoidea.**
  - ,, 2. **Batocrinoidea.**
  - ,, 3. **Actinocrinoidea.**

SUB-CLASS 2. DICYCLICA.

- Order 1. **Inadunata.**
  - Sub-Order 1. **Cyathocrinoidea.**
  - ,, 2. **Dendrocrinoidea.**
- Order 2. **Flexibilia.**
  - Grade 1. **Impinnata.**
  - ,, 2. **Pinnata.**
- ,, 3. **Camerata.**

PELMATOZOA in which epithecal extensions of the food-grooves, ambulacrals, superficial oral nervous system, blood-vascular and water-vascular systems, coelom, and genital system are continued exothecally upon jointed outgrowths of the abactinal thecal plates (*brachia*), carrying with them extensions of the abactinal nerve-system. The number of these processes is primitively and normally five, but may become less by atrophy. The brachia rise from a corresponding number of thecal plates, "radials (RR)." Below these is always a circlet, or traces of a circlet, of plates alternating with the radials, *i.e.* interradial, and called "basals (BB)." Through all modifications, which are numerous and vastly divergent, these elements persist. A circlet of radially situate infrabasals may also be present. Below basals or infrabasals there follows a stem, which, however, may be atrophied or totally lost.

---

[1] By F. A. Bather, M.A.

Although many Rhombifera simulate Crinoidea in the pentamerism of the theca or the possession of exothecal extensions of the food-grooves, yet in none are those extensions supported by plates that are clearly outgrowths from the abactinal system of thecal plates; in none is there the intimate correlation between brachia and radialia that obtains in the Crinoidea. This class therefore cannot be derived from the Rhombifera, as many structures might otherwise lead us to suppose; the presence of brachia also forms a clear distinction between it and Diploporita and Blastoidea. A further difficulty in tracing the origin of the Crinoidea is furnished by the occurrence of perfectly developed species in the Lower Cambrian, while representatives of all crinoid orders are plentiful in Ordovician rocks. Further research, however, may throw back the origins of other Echinoderm classes; in any case, negative evidence when Cambrian rocks are concerned counts for little.

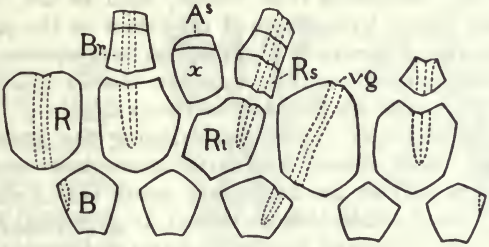


FIG. I.

Analysis of the cup and brachial elements of *Hybocystis problematicus.* The outlines of the food-grooves (*vg*) are dotted.

Certain features in some of the older Crinoidea seem to throw light on their ancestry. Such are the presence of hydrospires, comparable to those of *Codaster*, in *Carabocrinus* (p. 172) and *Hybocrinus* (p. 145); the presence in these and other genera of well-developed deltoids (Δ), over the edges of which pass the ambulacra, while the posterior Δ frequently shows signs of a hydropore (Fig. XXXVI.); the absence of a brachium from certain radials in *Baerocrinus* (Fig. LVII. 4); the greater development of three radials in many Inadunata Monocyclica (see p. 144). We are thus led to a form not unlike that which is actually presented by *Hybocystis*, Wetherby (1880), from the Ordovician of Kentucky (Fig. I.). This has 5 large subequal basals, 5 radials, and 5 deltoids. The anus lies between the posterior Δ and the radial circlet, being separated from the latter by a special anal plate (x). The right posterior radial is transversely bisected; its upper smaller portion (Rs) being pushed a little to the right by x. The striking peculiarity of this form is the continuation of the food-grooves over the thecal plates, as in Diploporita and Blastoidea. In the right and left antero-lateral rays these pass over the edges of the deltoids, over the radials, on to the underlying basals. In the anterior and the right and left posterior rays there are two ossicles, each as high as wide, supported on the summits of the radials; the grooves pass between the deltoids, over these ossicles, down on to the outer surfaces of the radials. These ossicles form exothecal, jointed outgrowths of the abactinal thecal plates; a deep notch on their inner surfaces, leading into the cup by a hole between the deltoids, suggests that they bore, besides the ambulacral structures, also extensions of the abactinal nerve-system. Therefore, although incipient, they constitute true *brachia*, such as are found in no Echinoderma except Crinoidea, and they show us the probable way in which brachia originated. Hydrospires have not been described; but, considering their occurrence in the closely allied *Hybocrinus* (Fig. XXXVI.), they are likely to be found along the radio-deltoid sutures, as in *Codaster*. Brachioles fringing the grooves do not seem to have been present, nor has a lancet-plate been observed. These facts, as well as the five basals, prove that *Hybocystis* is not an offshoot from Eublastoidea, as indeed its geological age forbids; but it may well be derived from early forms of Protoblastoidea. If *Hybocystis* be admitted as actually ancestral, then the development of brachia in only three rays sheds light on corresponding irregularities of development in many simple and ancient crinoids, connecting them in this respect with primitive Cystidea (see pp. 11, 53).

Another form suggestive of the connection of the Crinoidea with the Blastoidea is *Stephanocrinus*, Conrad (1842), Silurian of N. America and England. C. F. Roemer (1851), Joh. Müller (1853), and Pictet (1857), regarded it as a cystid; Etheridge & Carpenter (1883) and S. A. Miller as a blastoid; Dujardin & Hupé (1862) and Hall (1851) as a crinoid; Zittel (1879) as doubtfully a blastoid. Wachsmuth & Springer (1886) proved the presence of brachia, which make it unquestionably a crinoid, but said, "It agrees by its oral and anal pyramid with certain forms of the Cystids, while in its general habitus and in the position of the ambulacra it agrees with the Blastoids." *Stephanocrinus* (Fig. II.) has 3BB, 5RR, and 5Δ, arranged as in Eublastoidea, especially Codasteridae. The radial processes are often prolonged into spear-like spines (S), one in each interradius. Each ambulacral groove lies in a deep sinus between the deltoids and radial processes, and it is continued on to an arm, which rises from a single brachial at the end of the sinus, and immediately bifurcates, the groove forking with it. The edges of the deltoids meet beneath the groove, but a space for the mouth ("peristome") is left in the middle. This space, as well as the whole groove, is covered by ambulacrals; these often fuse into a single plate on either side the groove, where it passes over the oral surface of the theca, and form five plates, likewise often fused, over the peristome (*P*). The anus is between posterior Δ and the adjacent radial processes, and is closed by a valve of four to six small plates. Certain pits in a similar position in other interradii possibly are atrophied hydrospires (*h*). The ornament of the cup-plates is strongly reminiscent of that in Eublastoidea; but there are clearly marked axial folds passing up from the basals to the arm-facets, perhaps due to the greater development of the abactinal nerve-system in the brachiate form. There were neither brachioles nor a lancet-plate. *Stephanocrinus* undoubtedly belongs to the simplest and most primitive group of the Crinoidea, and it is hard to believe that its remarkable resemblances to Eublastoidea are merely homoplastic, especially since the position of the small basal is not one which usually occurs in other Crinoidea that have fused basals.

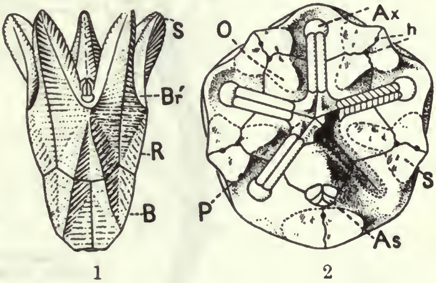


FIG. 11.

Stephanocrinus angulatus. 1, from anterior radius, × 2 diam.; 2, from oral surface, × 4 diam. (from Brit. Mus. E6715). *As*, anus, covered by plates; *Ax*, axillare, from which are supposed to spring two arm-rami; *Br′*, position from which these spring, between *S*, spines formed by radial processes, broken off in 2, and showing (*h*) supposed atrophied hydrospires; *P*, large covering-plates over the peristome, which is surrounded by the five orals or deltoids (*O*).

However the crinoid or brachiate stage in the history of the Pelmatozoa may have been reached, it will be useful to recapitulate here the common pelmatozoic characters as well as those distinctive of the Crinoidea, as manifested in **a normal crinoid of simple structure.** The specialisation of those characters will be shown historically in the systematic part; but since many structures have been produced or modified in the same way more than once, a general account of the processes may be given here. We can speak more decidedly on questions of development and internal anatomy in this class, since the differences between extinct and recent genera are not such as to hinder interpretation.

A normal Crinoid was thus described in 1821 by J. S. Miller, the founder of the class: "An animal with a round, oval, or angular column, composed of numerous articulating joints, supporting at its summit a series of plates or joints forming a cup-like body containing the viscera, from whose upper rim proceed five articulated arms, dividing into tentaculated fingers, more or less numerous, surrounding the aperture of the mouth, situated in the centre of a plated integument, which extends over the abdominal cavity, and is capable of being contracted into a conic or proboscal shape. Some species of these animals ascer-

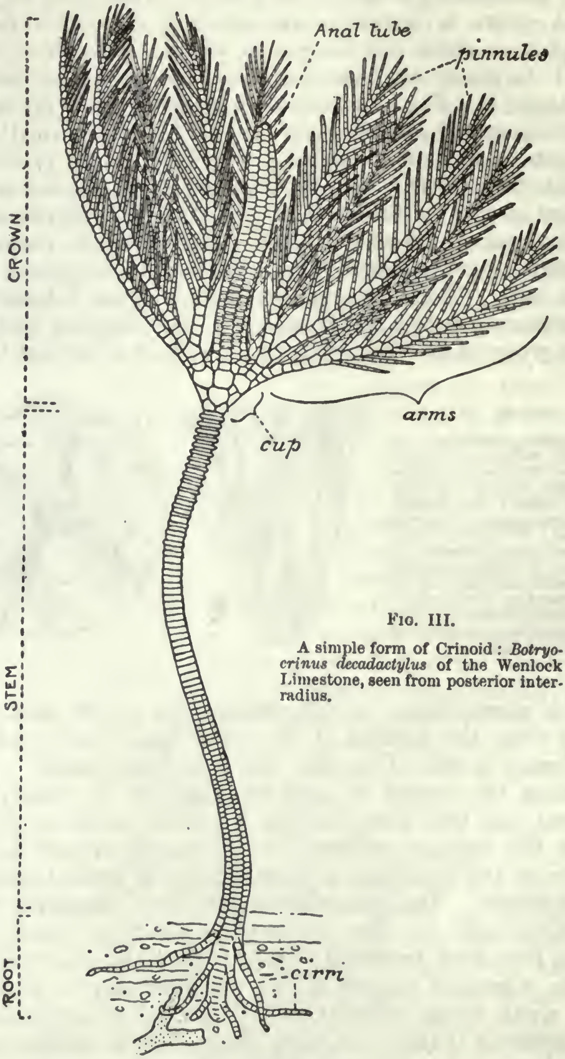


Fig. III.

A simple form of Crinoid : *Botryocrinus decadactylus* of the Wenlock Limestone, seen from posterior interradius.

tained to be permanently attached to extraneous bodies, whilst others appear to have been capable of locomotion." So little is amiss with this description, that we need do no more than translate it into modern terminology, as follows:—

A normal Crinoid (Fig. III.) consists of a "crown" (*corona*) attached by its dorsal (*i.e.* aboral) extremity to a "stem" (*columna*), which is fixed to the sea-floor or to some solid body by a "root" (*radix*). The crown consists of a *theca* (or calyx, in the sense of Wachsmuth & Springer) containing the viscera, and of 5 "arms" (*brachia*), which may be more or less branched. That part of the theca below the origins of the free arms is called the "dorsal cup" (or shortly "cup"); that part above the origins of the free arms, *i.e.* the oral surface, is called the *tegmen* (sometimes "disc," sometimes "vault," between which a distinction erroneously used to be imagined). The skeletal and many of the other systems have a radiate arrangement, of which 5 is the dominant number. Thus the whole animal can be divided into 5 corresponding and almost symmetrical sections, "pentameres," by 5 imaginary "perradial planes," starting from the vertical dorso-ventral axis and passing through the origins of the arms. The skeletal elements are either perradial or interradial in position.

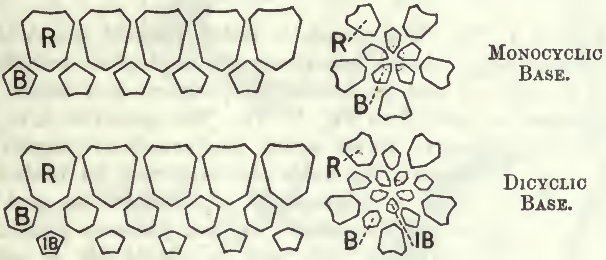


FIG. IV.

Imaginary analyses of the structure of the dorsal cup in two simple types of Crinoid.

The Dorsal Cup in its simplest form is composed of 2 or 3 circlets of 5 plates, those in one circlet alternating with the 5 in the adjacent circlet (Fig. IV.). Of these the most important are those that support the brachia, and to them the term *radialia* (RR) is restricted. The interradial plates below these are called *basalia* (BB), since in many crinoids they form the base and rest on the stem. In some crinoids a circlet of perradial *infrabasalia* (IBB) occurs beneath the BB (which latter are then called *parabasalia* by some writers). The former type of base is called "monocyclic"; the latter "dicyclic."

The Tegmen in its simplest form is likewise composed of 5 plates, *deltoidea* (Δ), here regarded as synonymous with *oralia* (O), alternating with the RR (Fig. V. 1). But there are nearly always also present "ambulacralia" (Amb or c.p), covering the grooves that lead between or over the apposed edges of the Δ to the brachia (Fig. V. 2). The mouth is either beneath the Δ or in a space between them; in the latter case it is covered by ambulacrals, often 5 in number and interradial in position, and taken to be orals by some writers (*P* in Fig. V. 3). The posterior Δ in many primitive forms seems to have been pierced by a hydropore, the walls of which may be folded so as to form a madreporite (cf. Stelleroidea and Echinoidea). The anus (*As*) lies between post. Δ and the adjacent RR, and is closed by a valvular pyramid, often surrounded by, or raised on, small plates.

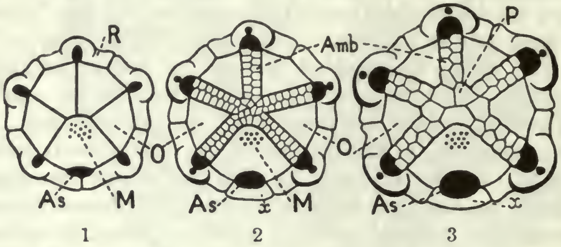


Fig. V.

Three stages in the evolution of the Tegmen. 1, orals only: 2. orals and ambulacrals; 3, orals, ambulacrals, and enlarged peristomial ambulacrals.

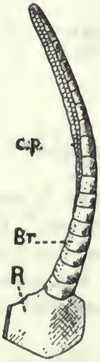


Fig. VI.

A simple, unbranched arm, that of *Hybocrinus*. *R*, radial; *Br*, brachial; *c.p*, covering-plates or ambulacrals.

The Brachia in their simplest form consist of a series of ossicles called *brachialia* (Br), which continue straight up from the radials (Fig. VI.). The surface of the radial to which the proximal brachial is attached is called the "radial- or arm-facet." Each brachial is rounded on the outer or dorsal surface, and grooved on the inner or ventral surface. The ventral or brachial groove contains the following soft parts, taken in order from ventral to dorsal (Fig. VII.). On the surface, the food-groove (*f.g*), lined with ciliated epithelium (*et*), which directs a stream of water towards the mouth; an epithelial nervous band (*n*1) stretching from the superficial or oral nerve-system; a blood-vessel (*b*), "radial pseudhaemal canal"; a water-vessel (*w*), which gives off tubes (*p*) to a series of *podia* or "tentacles" (*t*) that fringe the food-groove and subserve sensation and respiration; two "subtentacular canals" (*s.t.c*), extensions from the body-cavity; a canal containing the genital cord or rachis (*g.c*); and a "coeliac canal" (*c.c*). On either side of the water-vessel, beneath the tentacles, is a senso-motor nerve (*n*2), giving off branches to the muscles of the water-canals and to sensory papillae (*s*) on the tentacles. Below all these, in a special groove on the very floor of the main brachial groove, lies another nerve, the "axial cord" (*a.c*), proceeding from the aboral or dorsal motor nerve-system; the groove in which this lies is often (as in Fig. VII.) separated from the brachial groove during individual development by an outgrowth of stereom, and is then known as the "dorsal" or "axial canal" (Fig. VIII.). The axial cord sends off branches (*n*3) to all the muscles of the arms, and to supposed sensory endings in the ectoderm (*ed*), and is connected with the subtentacular nerves. All these soft structures in the ventral groove are protected by covering-plates (*c.p*), also

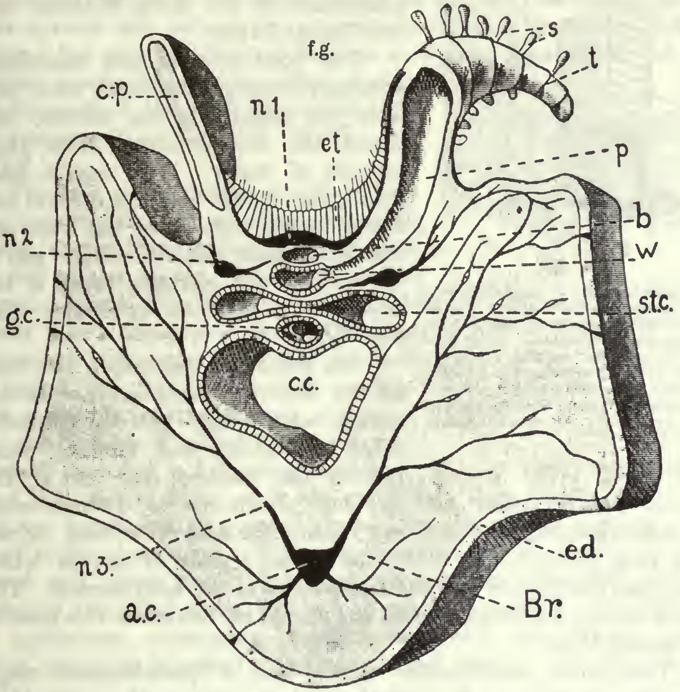


Fig. VII.

Diagram of solid section of a Crinoid arm. For explanation of letters see adjoining text.

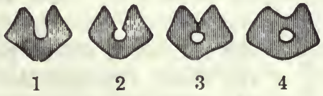


Fig. VIII.

Stages in the separation of an axial canal, exemplified by brachials of *Gissocrinus goniodactylus.* 1 is youngest; 4, oldest. × 6 diam.

called "ambulacrals" (Amb), which can open or close as occasion demands (Fig. IX.).

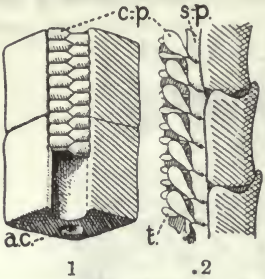


FIG. IX.

Ambulacrals. 1, ventral view of two brachials of *Gissocrinus squamifer*, with c.p closed above and removed below, × 8 diam. 2, side view of brachials of *Antedon basicurva*, with c.p open, exposing tentacles (*t*); c.p are supported on side-plates or adambulacrals (*s.p*), between which are seen notches for sacculi (p. 137), × 15 diam.

We may now trace the various extensions of the Body Systems into the Thecal Cavity.

The food-grooves and associated structures, except the axial cord, pass over the tegmen to the mouth, into which the food-grooves drive their streams of water. The mouth leads into a gut, which makes a dextral coil down to the bottom of the cup, and then rises along the side of the cup to the anus; this system, then, is not affected by radiate symmetry (see Fig. VII. p. 9).

The epithelial nerves on the floor of the food-grooves also pass to the mouth, where they join an epithelial ridge encircling the mouth; from this "oral ring," nerves pass to the walls of the gut. The paired subtentacular nerves run down to a subepithelial, "circumoesophageal nerve-ring," below the oral nerve-ring. From this ring proceeds, in each interradius, a pair of nerves which innervate the tegmen and the mesenteries of the body-cavity. This nerve-system is connected with the aboral nerve-system in a manner explained below.

The radial pseudhaemal canals join a "pseudhaemal ring" round the oesophagus beneath the oral nerve-ring; these structures are hard to distinguish, and even in other classes, where they are better developed, their origin is not yet clear. There is, however, surrounding the oesophagus a "lacunar plexus" belonging to what is generally called the blood-vascular system. The circumoesophageal ring is connected with two vascular trunks leading from the plexus that surrounds the intestine and that absorbs nutrient substances therefrom; these substances appear to be worked up into corpuscles by a "spongy organ" in the oesophageal ring. The ring is also connected with a plexus that passes down the vertical axis of the theca, through the coil of the gut, to the base; this surrounds the "axial organ" (*vide infra*).

The water-vessels (perradial ambulacral canals) meet in a circumoesophageal water-vascular ring (*hydrocircus*); these structures have longitudinal muscle-bands, as well as muscle-fibres traversing the lumen; no ampullae or valves are differentiated, as they are in forms where this system has a locomotor function. In so simple a crinoid as is here in question, there is good reason to believe that the water-ring opened into the body-cavity by a single ciliated canal in the posterior interradius; and that the body-cavity communicated with the exterior by a single hydropore in post. Δ, sometimes merged in the anal opening (as probably in Blastoidea). This system was not as yet completely affected by radiate symmetry; but in some forms it became so by the development of a similar canal with corresponding hydropore in each of the other interradii (Fig. X., compare Figs. XXXIV., XLVI., and CXIV.).

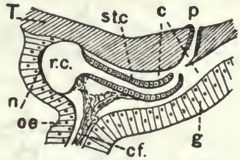


FIG. X.

Water-pore of *Rhizocrinus lofotensis*. Section through part of an interradius (× 180) simplified from Ludwig. *c*, coelomic space; *cf*, connective tissue fibres; *g*, wall of gut; *n*, circumoesophageal nerve; *oe*, oesophagus; *p*, pore; *r.c*, ring canal; *st.c*, stone canal; *T*, stereom of oral.

The two subtentacular canals of each arm enter a division of the coelom that passes down the vertical axis through the coil of the gut, and is known as the "axial sinus." The dorsal coeliac canal passes into a division of the coelom that surrounds both axial sinus and gut, and is called the "peri-intestinal cavity." The remainder of the coelom, surrounding the latter, is called the "subtegumentary cavity." All these divisions of the body-cavity are lined by endothelium, and are separated from each other, as well as penetrated, by connective tissue, in which spicules are often richly developed. From the peri-intestinal cavity, at its aboral end, there are in this way cut off five chambers, which surround the axial sinus, and are themselves covered on all sides by epithelium, containing ganglion-cells and nerve-fibres; the whole structure is called "the chambered organ" (see Fig. XX. p. 24).

The genital rachis of each arm is connected with a complex of twisted, fine canals, called the "axial organ" (see p. 23). This passes down the axial sinus, widening in the middle of its course, and then narrowing to a thin strand as it passes between the five chambers just mentioned.

The axial nerve-cord of the arm does not, as all the organs yet dealt with, pass to the oral centre, but enters the theca over the radial. If there is a separate axial canal, it may be continued through the radial facet into the substance of the thecal plates. The cords ultimately pass into the epithelial covering of the chambered organ, but their passage is not a direct one (Figs. XI. and XII.). Each cord is really a double structure, connected at intervals by chiasmas, and so soon as it enters the radial it divides into two branches, one of which proceeds to the basal on the right, the other to that on the left. In addition the branches are connected with each other and with those of the other radii by a series of commissures that form rings all round the cup. One such ring is at the level of the radials. If the crinoid have a monocyclic base, the cords that pass to the basals join one another in a ring immediately surrounding the chambered organ, the lobes of which in this case correspond with the basals, *i.e.* are interradial. If the base be dicyclic, the ring forms a commissure at the level of the centres of the basals; and from these points the cords again fork towards the adjacent infrabasals, where they join in another ring round the chambered organ, the lobes of which in this case correspond with the infrabasals, *i.e.* are

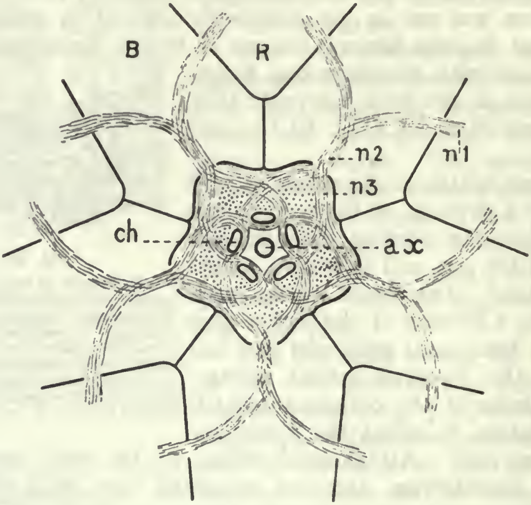


Fig. XI.

Course of axial nerve-cords in *Isocrinus*. Diagrammatised from sections figured by P. H. Carpenter. *B*, basal; *R*, radial; *ax*, axial organ; *ch*, five chambers of chambered organ; *n*1, nerve-cord from *R* to *B*; *n*2, cord passing down *B*; *n*3, cord from *B* to radially placed lobes of chambered organ.

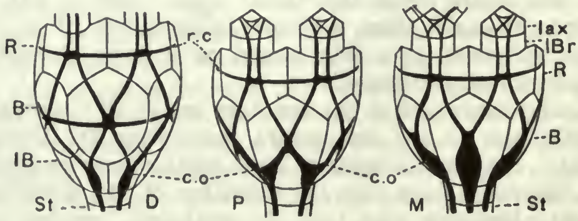


Fig. XII.

Course of axial nerve-cords in Dicyclic (*D*), Pseudomonocyclic (*P*), and Monocyclic (*M*) Crinoids. *c.o*, lobes of chambered organ, the connecting nervous sheath omitted for greater clearness; *r.c*, ring commissure in radials; other letters as usual.

radial. Nerves from these cords are given off to the stroma of the cup-plates. This system, as experimentally proved, chiefly by W. B. Carpenter (1876 and 1884), in opposition to the scientific opinion of his time, is a senso-motor nerve-system, governed from the nervous capsule of the chambered organ. By means of the commissures the motion of all muscles is correlated. Primitively the cords lie on the inner surface of the cup; they then become bordered by ridges of stereom, and finally enclosed within the cup-walls. Branches from these nerves unite with the interradial nerves that proceed from the circumoesophageal nerve-ring.

To turn to the Stem. We have already traced its probable origin as an evagination of the many-plated theca of Amphoridea, and the gradual introduction of order into the irregular plates (p.48). In the pentamerous Crinoidea, these naturally became subjected to pentamerism; and evidence of many of the older crinoids shows that the plates were at first hexagonal and arranged in alternating circlets of 5, just as plates of the theca (Fig. XIII.). The next stage was that in which the plates no longer alternated, but were arranged in horizontal rows divided by five longitudinal sutures. Finally, the pentameres of each row became fused to form a "columnal," still pierced by a wide lumen. This regularity was perhaps connected with the extension into the lumen of a vessel from each of the five lobes of the chambered organ, with its nerve-sheath (axial cord); the five cords surrounded a prolongation of the axial organ. In a monocyclic crinoid the axial cords would be interradial, as are the lobes of the chambered organ, while the pentameres would alternate with the basals and be radial. In a dicyclic crinoid the cords would be radial, the pentameres interradial. The exterior angles of the stem usually correspond with the pentameres, but not always. The cirri, or side-arms of the stem, correspond, for reasons that will appear presently, with the axial cords. The lumen of the stem is often split up into grooves by ingrowths of stereom; and these grooves primarily contain the axial cords, and may even form closed canals containing the cords, but this correspondence is not inevitable. The so-called "law of Wachsmuth & Springer,"

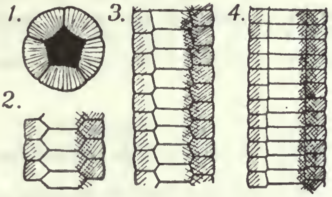


FIG. XIII.

Evolution of Pentamerism in the Stem. 1, joint surface of a columnal composed of five sections, which alternate with the angles of the stem-lumen; 2, portion of a stem composed of hexagonal alternating plates, which in 3 become arranged more definitely in horizontal rows; 4, continuance of the process results in columnals of five pentameres. The figures are of *Botryocrinus* stems (after Bather).

summarised in the annexed diagram (Fig. XIV.) and table, is in itself empirical, applicable only to pentagonal stems or lumens, and even then liable to exceptions (marked * in table); but by attending (as is here done) chiefly to the relations of the axial cords, we shall have a surer guide for discrimination between monocyclic and dicyclic crinoids in the many doubtful cases that occur.

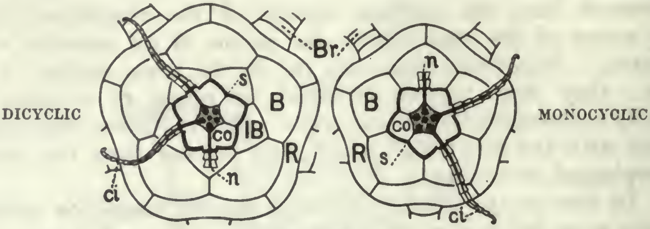


Fig. XIV.

Comparison of the Dicyclic and Monocyclic base. *B*, basal; *Br*, brachials marking the five rays; *ci*, cirri, only three out of the five are shown; *co*, pentameres of column; *IB*, infrabasal; *n*, nerves going to cirri from extensions of capsule; *R*, radial; *s*, sutures between pentameres of stem.

	Dicyclic.	Monocyclic.
BB [lobes of capsule in Monocyclica] .	Interradial	Interradial
IBB [lobes of capsule in Dicyclica] .	Radial	...
Pentameres of stem (*p*) . .	Interradial	Radial
* Outer angles of stem . . .	Interradial	Radial
Vertical sutures of stem (*s*) . .	Radial	Interradial
* Sides of stem	Radial	Interradial
* Angles of lumen of stem . .	Radial	Interradial
Cirri, when present (*c*) . .	Radial	Interradial
[Axial cords]	Radial	Interradial

The primitive crinoid is attached by the distal end of its stem; and it is supposed by many, from the evidence of the embryo *Antedon* (Fig. XV.), that there is developed at that point a special fixing plate, to which they apply the term "dorso-central," which must not be confused with "centro-dorsal" (see especially the writings of P. H. Carpenter). Palaeontology does not lead us to regard such a structure as primitive, or to ascribe to it any morphological importance. As a rule, skeletal growth takes place at the distal end of the stem after two main plans: (1) Deposition of solid, unjointed stereom, around the distal columnals, forming an encrusting plate or mass (Fig. CXIII. 2); this occurs on rocky bottoms. (2) Outgrowth of jointed branches from the plated end, forming "radical cirri," often with traces of polymeres like those of the primitive stem, often very long and branching again, and always with a lumen which contains an extension of the axial cord (Fig. CXVI.); this is adapted to a muddy bottom. The radical cirri arise from the vertical suture-lines of the stem, by the intercalation and outgrowth of small plates, and the extrusion of the axial cord (Fig. XVI. 3). In the course of race-history the cirri gradually appear higher and higher up the stem (Fig. XVI. 1), and at the same time become shorter, more mobile, and eventually arranged in whorls (Fig. XVI. 5). At these levels the axial cords of the stem swell out, forming a repetition of the chambered organ (Fig. XVI. 4).

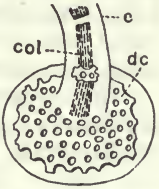


Fig. XV.

Distal end of stem of larval *Antedon bifida*, after Wyville-Thomson, × 20 diam. *col*, fascicular stereom of column; *dc*, "dorso-central"; *e*, ectoderm.

The columnals are rarely all of the same height; certain conspicuously larger ones, including those that bear cirri, are termed

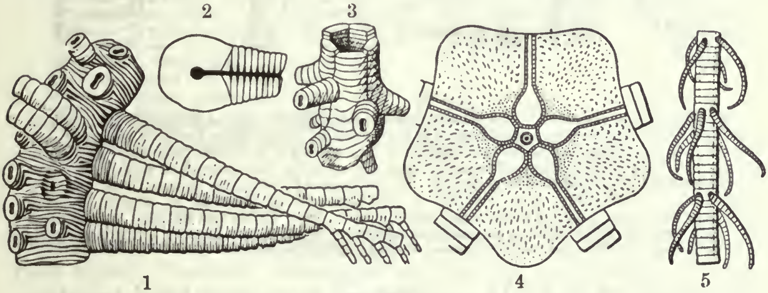


Fig. XVI.

Evolution of cirri. 1, part of stem of a Silurian crinoid with large, branching cirri (Brit. Mus. E1354). 2, section across stem of a Carboniferous crinoid, showing branch from axial canal to cirrus (Brit. Mus. E6708). 3, root of *Barycrinus*, with cirri originating between pentameres (modified from Wachsmuth & Springer). 4, section across stem of *Isocrinus Wyville-Thomsoni* at level of cirrus-whorl, the central portions disproportionately enlarged for greater clearness. 5, part of stem of *Isocrinus decorus*, with cirri in whorls of five.

"nodals"; those between them "internodals" (Fig. XVII. 1). Nodals are the first columnals to be formed during growth; internodals are subsequently intercalated between them, and again fresh internodals between the first formed internodals, and so on. Fresh nodals are developed at the proximal end of the stem, so that in that region are more nodals, while distally are more internodals (Fig. XVII. 2 and 3). In one type nodals are introduced immediately beneath the base of the cup, so that the proximal columnal is always the youngest. In another type the proximal columnal is one of the first formed, and remains attached to the cup, new nodals being introduced below it (Fig. XVII. 4-7). This proximal columnal is called *article basal* by P. de Loriol, and "centro-dorsal" by others, erroneously. It is here called the *proximale.*

The Connection between the Elements of the Crinoid Skeleton is primarily by means of the fibrils of the stroma in which they are deposited. This condition persists in the "primitive suture," and from it development proceeds in the direction of either greater rigidity or greater flexibility. Towards rigidity we have: (1) "Close suture," in which the fibres are short, and their ends surrounded by denser layers of stereom on the apposed surfaces of the ossicles, which are thus closely and immovably fitted together, though separable by alkalies. (2) "Syzygy," a special case of close suture between brachials or columnals (Fig. XVIII. 2, 3, and 4), in which the upper ossicle, "epizygal," bears a pinnule or cirri, as the case may be, and the lower one, "hypozygal," bears none. (3) "Anchylosis" or fusion, when two ossicles are immovably cemented by an unbroken deposit of stereom, which, however, is less solid than that of the plates themselves. Towards flexibility we have: (1) That form of "loose suture" in which the stroma-fibrils lie at right angles to the suture, and the stereom is thrown into corresponding folds (cf. pore-rhombs of cystids), or that form in which there is a slight facet, either smooth or striated (Fig. CXI. 3), or interlocking crenulations (Fig. XVIII. 1). (2) "Imperforate articulation," in which there is a slight facet, or a toothed

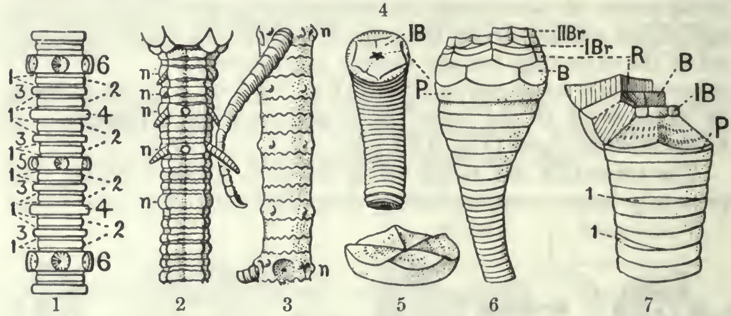


Fig. XVII.

The Relations of the Stem. 1, portion of stem of *Gastrocrinus patulus* (modified from Jaekel), the latest formed columnals are numbered *1*, the oldest *6*; *5* and *6* bear cirri. 2, proximal, and 3 distal, regions of stem of *Isocrinus decorus* (cf. 5 in Fig. CI.), *n*, nodals (modified from P. H. Carpenter). 4, proximal region of stem of *Onychocrinus* (after Wachsmuth & Springer), showing infrabasals (*IB*) fused to proximale (*P*). 5, proximale of *Apiocrinus elegans*, Defr., showing depressions for *BB* (Brit. Mus. E6711). 6, cup and part of stem of *A. elegans*, showing proximale and other enlarged columnals (based on Brit. Mus. E6709 and E6710). 7, portion of cup and stem of *Millericrinus polydactylus* (modified from P. de Loriol), showing minute infrabasals attached to proximale, also new columnals forming (*1*).

articular surface (Fig. XVIII. 5); the fibrils are at first developed into elastic ligaments, and later into true muscles. (3) "Perforate articulation," in which there is a highly developed facet, with fulcral ridge, ligamentar depressions, and muscles innervated from an axial cord which perforates the ridge (Fig. XVIII. 6).

In such a simple crinoid as that under discussion the cup-plates would be united by close suture; the tegminals, probably by primitive suture, or loose suture of the rhomb type; the brachials, by imperforate articulation, perforate being a later development; the columnals, by loose suture of the striate type.

The Skeletal Elements of a crinoid may be thus classified: "Primary Elements," the first to be developed in both ontogeny and phylogeny, divided into — "abactinal," developed on the right or aboral coelom, and directly innervated from the chambered organ, viz. columnals, cirrals, IBB, BB, RR, Br, and pinnulars (*vide infra*); "actinal," developed on the left or oral coelom, and connected with the various oral ring-systems, viz. Δ (orals) and ambulacrals (Chapter VIII., Fig. X.). "Secondary or Supplementary Elements," which may be intercalated between the primary pieces; these have not yet been discussed; they include "interbrachials" (iBr), "interambulacrals" (iAmb), "interaxillaries" (iAx), some "anals," and a few others of no special importance.

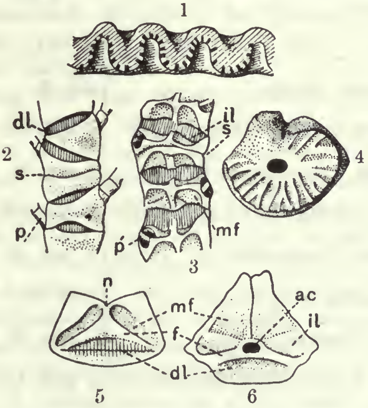


FIG. XVIII.

Forms of Joint. 1, sutural margin of cup-plate of *Marsupites* (original). 2, brachials from dorsal side, × 10. 3, ditto from ventral side, $\times \frac{15}{2}$. 4, distal face of IIBr$_3$, a hypozygal, $\times \frac{15}{2}$. (2, 3, and 4 are of *Antedon bifida*, after W. B. Carpenter.) 5, articular facet of radial of *Pisocrinus ollula*, × 3 (after Bather). 6, articular facet of radial of *Bathycrinus aldrichianus*, × 8 (after P. H. Carpenter). *ac*, axial canal for nerve; *dl*, dorsal ligament; *f*, fulcral ridge; *il*, interarticular ligament; *mf*, muscle fossa; *n*, notch for axial nerve; *p*, pinnule; *p'*, pinnule-facet; *s*, syzygy.

The terms "proximal" and "distal" are reckoned from the plane separating stem from crown, so that the infrabasals and top columnal are the proximal elements of crown and stem respectively. The actinal elements, however, start from the oral centre as proximal point.

For orientation the crinoid is placed in its natural position, mouth upwards, and is viewed from the anal side. The anal interradius is then posterior; the radius opposite it is anterior;

right and left correspond with the right and left of the observer. To preserve this orientation when the crown is viewed from above, the anal side must be nearest the observer (downwards in a figure); when viewed from below, the anal side must be away from the observer (upwards in a figure). Such is the rule followed in the drawings illustrating this book, while in the various analyses the anterior radius is always placed on the right of the figure. Various modes of designating the radii have been attempted. To extend to the Crinoidea Lovén's Echinoid numeration, is to postulate an homology that is far from proven. The annexed table compares with other systems the symbols here used :—

Orientation as above described.	Symbols here used.	P. H. Carpenter in *Challenger* Reports and Blastoid Catalogue.		Lovén for Echinoidea, Jaekel for Crinoidea.	Ordinary Nomenclature of Echinoidea and Stelleroidea in Natural Position.	
Anterior Radius	ant. R.	A		III.	ant.	Trivium.
Right Anterior Interradius	r. ant. IR.	A-B	Left.	3	l. ant.	
Right Antero-lateral Radius	r. ant. R.	B		IV.	l. ant.-lat.	
Right Postero-lateral Interradius	r. post. IR.	B-C		4	l. post.-lat.	
Right Posterior Radius	r. post. R.	C		V.	l. post.	Bivium.
Posterior Interradius	post. IR.	C-D		5	post.	
Left Posterior Radius	l. post. R.	D	Right.	I.	r. post.	
Left Postero-lateral Interradius	l. post. IR.	D-E		1	r. post.-lat.	
Left Antero-lateral Radius	l. ant. R.	E		II.	r. ant.-lat.	Trivium.
Left Anterior Interradius	l. ant. IR.	E-A		2	r. ant.	

We have now run through the chief characters of a normal crinoid of simple structure. Few are so simple as this, but various **modifications** have occurred **in the history of the class**, some perhaps only once, others at different geological periods in races of diverse origin. Some of these, especially when of importance for classification, must now be discussed.

Some crinoids have a Dicyclic, others a Monocyclic Base (p. 99). The value of this in classification is disputed. Among various early genera, placed by Wachsmuth & Springer in a single family (Reteocrinidae), some are with, some without infrabasals, having the angles of the stem-lumen respectively radial and interradial. But the yet simpler genera, from which presumably these genera descended, probably differed in the same way; and resemblances, undoubtedly of secondary nature, should not lead us to place together forms of diverse origin. The distinction to be drawn between monocyclic and dicyclic genera is more obvious in the simpler crinoids; but here too there are parallel stages passed through—the monocyclic *Iocrinus* and *Heterocrinus* (p. 145) correspond with the dicyclic *Merocrinus* and *Ottawacrinus* (p. 178) respectively. Since the presence or absence of infrabasals is correlated with the radial or interradial position of the lobes of the chambered organ, the derivation of one type from the other involves more change than the mere atrophy or appearance of certain plates. Hence monocyclic and dicyclic genera should not be placed in the same line of descent, unless this change can be proved: there is no reason why they should not have been independently evolved. The origin of Dicyclica from Monocyclica is, in fact, opposed by the available evidence; but Monocyclica may conceivably have been derived from Dicyclica in one of two ways, outlined in the next two paragraphs.

There are, especially among the later crinoids, several genera known as "pseudomonocyclic," because though infrabasals are invisible or absent, at all events in the adult, the evidence of the axial cords (*e.g.* in *Rhizocrinus*) of palaeontology (e.g. *Apiocrinus* and *Pentacrinus*), or of embryology (e.g. *Antedon*), demonstrates the existence of infrabasals either in the young or in near ancestors. Discoveries of this nature have strengthened Wachsmuth & Springer's law by affording a rational explanation of apparent exceptions. But suppose secondary growth of stereom to occur in a pseudomonocyclic genus, converting the angles of the stem from interradial to radial, and the angles of the stem-lumen from radial to interradial. Then, if recent examples were known, the law, as emended above (p. 106), might be applied successfully; but it would not tell the truth if only fossils were available, and the crinoid would pose as monocyclic. Such changes are actually observed in the growth of *Antedon*, while in *Isocrinus*, which other facts prove pseudomonocyclic (Fig. XI.), the angles of the stem-lumen in the proximal region are interradial, as if the genus were truly monocyclic, though the downward prolongations of the chambered organ are radial. In *Glyptocrinus Fornshelli* the angles of both stem and axial canal are radial; since there are actually no infrabasals, we may suppose secondary ingrowth of stereom, and this is confirmed by S. A. Miller's description of the columnals (1874).

The changes just described leave the essential distinction between monocyclic and dicyclic genera untouched (as shown in Fig. XII.); and among the earliest crinoids there is little evidence of pseudomonocyclic forms. There is, however, a possibility that the change from Dicyclic to Monocyclic may have taken place, not by compression and atrophy, but by torsion and fusion. Many monocyclic genera of Ordovician and Silurian age have some radials (usually r. post., r. ant., and l. ant. RR) transversely bisected; the upper part is called "super-radial" (R*s*); the lower part, "inferradial" (R*i*), (see Fig. LVIII.). Now, in some dicyclic genera (e.g. *Ottawacrinus*, Fig. XCVI.), perhaps in consequence of the introduction of fresh plates in the anal interradius, the radials are shifted to right and left so as to lie almost vertically above the basals. The suggestion then is that the inferradials and basals of Monocyclica represent basals and infrabasals respectively of Dicyclica. If then the R*s* and R*i* fuse, a truly monocyclic type is produced with one circlet of BB and one of RR. One obvious objection to this theory is the presence in many Dicyclica of a plate (the radianal, RA), which is now generally regarded as a slightly modified inferradial (r. post. R*i*), (Fig. XXVI.). Other objections to this and similar views, based by P. H. Carpenter (1878) on alleged homologies with the apical system of Echinoidea, have, it is true, been somewhat discredited by modern embryological and palaeontological research. Nevertheless, for the present the gulf between Monocyclica vera and Dicyclica is unbridged, and must be recognised in classification.

The dorsal cup of a simple crinoid consists of two or three circlets, but there is often a tendency for the proximal brachials to be so joined to the radials and to one another as to form part of the cup (Fig. XIX.). There is, however, a supposed morphological distinction between these "fixed brachials" ($\overline{\mathrm{Br}}$) and the radials: the latter are developed in the *Antedon* larva as expanded sieve-like films; but all brachials begin as "imperfect rings, which soon become filled up with lengthening fasciculated tissue" (P. H. Carpenter, 1884; see Fig. XIX.). In a form where many brachials enter the dorsal cup, it is convenient to have a common tern for the primitive elements of the cup (IBB, BB, RR): some call them the "apical system," postulating a homology with the plates so called in Echinoidea; the old term *patina* is shorter and safer.

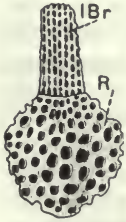


FIG. XIX.

R, radial, cribriform stereom; *IBr*, primibrach, fasciculate stereom; in *Antedon bifida*, × 75. (Based on figure by W. B. Carpenter.)

To understand the extension of the cup beyond the patina, it is necessary first to study the Arms or *Brachia* (Fig. XX.). These are rarely single. The first step in advance is a bifurcation, constantly repeated in a regular manner (regular dichotomy or isotomy). Modifications of this occur through the suppression of a bifurcation at definite points (irregular dichotomy or heterotomy). In each half of the arm, the first branch on the right, then the first on the left, and so on, may be smaller than the other branch. Thus there arises a main trunk giving off smaller branches right and left alternately. These smaller branches may themselves undergo a similar process, and so form armlets (*ramuli*) borne by the main arm-branch (*ramus*). When the ramules cease to branch themselves, and are regularly placed on alternate sides of successive brachials of the main branch, they are called *pinnulae*, and the arm is "pinnulate." This process of evolution has been phylogenetically traced in *Botryocrinus* (Fig. XXI.), while the primitively dichotomous origin of the pinnules may be seen in the developing *Antedon*. The pinnule, as P. H. Carpenter said, is an arm in miniature; it differs in nothing but position from the small end-branches of a simple dichotomous arm; but, in a pinnulate arm, it differs from the ramus by the restriction to it of the fertile portions

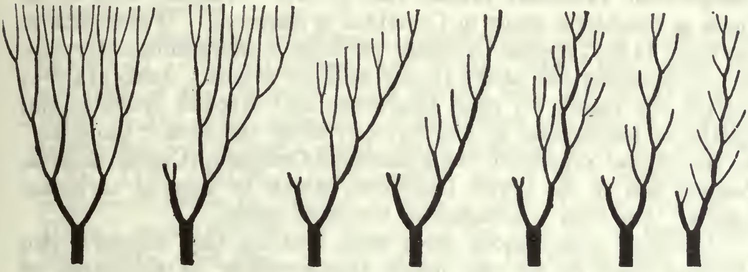


Fig. XX.

Specialisation of arm-branching. 1, a non-pinnulate, regularly dichotomous arm (isotomous); 2, a less regular dichotomous arm, a type common in Cyathocrinoidea; 3, 4, two stages in the evolution of unilateral heterotomy; 5, 6, 7, three stages in the evolution of bilateral heterotomy, culminating in pinnulation. For other types, see Fig. CX.

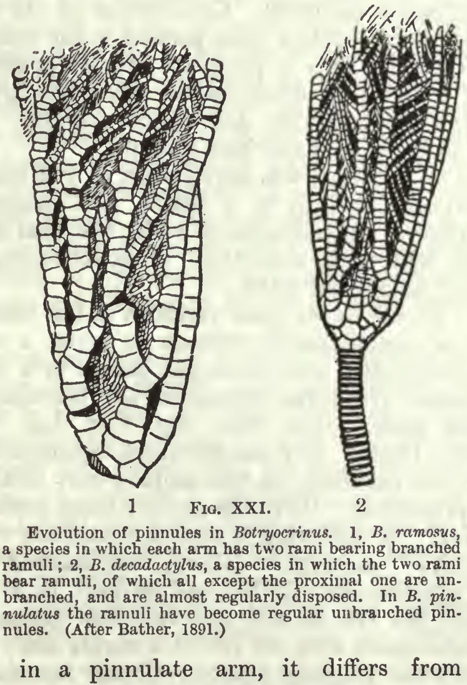


Fig. XXI.

Evolution of pinnules in *Botryocrinus*. 1, *B. ramosus*, a species in which each arm has two rami bearing branched ramuli; 2, *B. decadactylus*, a species in which the two rami bear ramuli, of which all except the proximal one are unbranched, and are almost regularly disposed. In *B. pinnulatus* the ramuli have become regular unbranched pinnules. (After Bather, 1891.)

of the genital rachis. The pinnule differs in origin, and probably in structure and function, from the brachiole, which is an independent exothecal process (see p. 41). Whether such structures as brachioles occur in Crinoidea is disputed. Wachsmuth & Springer (1897) appear to regard pinnules as independent developments, rejecting the above theory of their origin. Jaekel (1894) accepts the theory for most Inadunata and Neozoic crinoids, and speaks of the organs as ramuli, restricting the term "pinnulae" to the similar organs of the Palaeozoic Camerata (Cladocrinoidea, Jaekel) and to the cystid brachioles, which he regards as homologous. His view is admissible, but lacks proof.

In simple dichotomous arms, each brachial that supports two branches does so by two upper sloping sides, or shoulders, of equal size, each notched by the ventral groove, and pierced by the axial canal, which branches with the arm. Such a brachial is called *axillare* (ax), and all that part of the arm borne by any single axillary is a "dichotom." The branches of the axial cord are united at their bifurcation by a criss-cross of nerve-strands (*chiasma*) serving to correlate their activities. As the size of one half of a dichotom is reduced, the supporting shoulder of the axillare is narrowed. Continuance of the process tends to bring the wider shoulder more parallel to the under joint-surface of the axillary. Thus a pinnulate arm of primitive structure consists of a series of axillaries in which the alternate right and left shoulders are wide and almost parallel, while the others are greatly reduced and bear pinnules.

A pinnulate arm may consist of two rami, or each ramus may bifurcate just as in a simple arm, though never to the same extent. The axillaries on which the rami fork remain unmodified, and with equal shoulders. It is convenient to distinguish these as "main-axils" (Ax).

Owing to the great variation in the branching of the brachia, it is extraordinarily difficult to devise a consistent terminology, or to denote any particular ossicle in a concise and intelligible manner (for fuller discussion, see Wachsmuth & Springer, 1897; and Bather, *Ann. Mag. Nat. Hist.* Jan. 1892; and *Geol. Mag.* July 1898). In a non-pinnulate dichotomous arm all brachials up to and including the first axillary may be styled *primibrachialia* or "primibrachs" (IBr), the axillary being distinguished as "primaxil" (Iax); the following Br in each branch are "secundibrachs" (IIBr), with a "secundaxil" (IIax); then succeed "tertibrachs" (IIIBr), "quartibrachs" (IVBr), and so on. In a pinnulate dichotomous arm the IBr do not as a rule bear pinnules, and are therefore homologous with the IBr of a simple arm; but of the next series only the proximal brachial of each ramus is strictly homologous with the IIBr of a simple arm, the pinnule borne by it, together with the next Br, representing the IIIBr of a simple arm. To use the same terms is especially perplexing in intermediate forms; but solutions of the difficulty, though proposed, have not gained general approval.

For descriptive purposes, a dichotomous arm is viewed from the dorsal, *i.e.* aboral surface, and "right" and "left" equal right and left of the observer. The mediad rami are called interior; those to the sides, exterior. A particular brachial in any series is denoted by placing a small Arabic numeral after the symbol—IIBr$_4$, IVBr$_6$, IIIBr$_5$. The number of Br in a series may be expressed either by stating it with a large Arabic numeral, *e.g.* IIIBr,7, and IIBr,10; or by giving the number of the axillare, thus IIIax$_7$, and IIax$_{10}$. The ossicles of the distal rami which do not branch again are called "finials" (F).

The ambulacrals (Amb)[1] necessarily branch with the brachials, and the several series or orders may be designated as IAmb, IIAmb, etc. Their simplest form is that of a line of small plates on either side the groove, capable of being raised or depressed; and when closed, meeting in the median line by a zigzag suture due to their alternating arrangement. They vary in size, both absolutely, and relatively to the brachials. Each ambulacral may be divided by one or more tranverse sutures, parallel to the long axis of the arm; this produces the appearance of short pinnules, for which these structures have been mistaken by more than one author. The transverse sutures may come to lie at an angle, and the portions to alternate with one another. Thus arose the side-plates or adambulacrals, which are a persistent feature in many of the later crinoids (cf. Fig. IX. 2). There may also be developed minute but distinct ossicles beneath the outer covering-plates and alternating with them. The complicated structure thus developed in *Cyathocrinus* and *Gissocrinus* has been exquisitely worked out and illustrated by G. Liljevall (Bather, 1893, pls. vii.-ix.).

Brachia, rami, ramuli, and pinnulae, in which the ossicles lie in a single row, with more or less parallel joints, are termed "uniserial." Simple arms in Crinoidea are always uniserial. Pinnulate arms undergo a modification. Since in such arms the joints slope alternately to right and left (p. 114), the brachials tend to assume a wedge-shape; in process of growth of either the individual or the race, a complete wedge-shape is assumed, so that the joint-lines between the ossicles form a "zigzag." Lastly, the brachials come to lie in two alternating rows, in which case the arm is termed "biserial." This development doubles the number of pinnules in a given length of arm, and thus aids the collection of food. The axial cords and ventral groove at first swing from side to side; but this would be almost impossible in biserial arms, so here a common straight ventral groove is formed, and the axial cord lies at the bottom of it. The change from uniserial to biserial, just as the evolution of pinnules, begins in both ontogeny and phylogeny at the growing tip of the arm, and proceeds gradually proximalwards (Fig. XXII.).

---

[1] The terms "ambulacral" and "adambulacral" must not be held to imply any homology with elements thus named in Stelleroidea and Echinoidea.

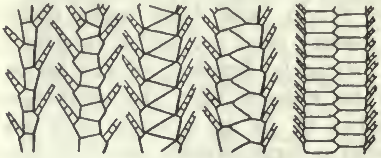


FIG. XXII.

Evolution from uniserial, through zigzag, to biserial brachials.

Still further development occurs in the Camerata. The adjacent right and left ossicles of a biserial arm may fuse, so as to form a compound brachial, and this necessarily bears two pinnules, one on either side. Further than this, it appears as though two or more compound brachials could fuse, and so form a triply compound ossicle bearing two or three pinnules on either side. At the same time, the pinnulars themselves may come to lie in zigzag or biserial fashion, in the same way as do the ossicles of so many cystid brachioles. It is this structure that influenced Jaekel in his distinction between "pinnulae" and "ramuli" (*supra*); but the facts are explicable as the final stage in a regular evolution (Fig. LXXIX.).

Fusion of brachials either laterally, or in vertical series, or both, may occur in any crinoid race in which it proves advantageous. In some *Gissocrini* the IIBr, and possibly IIIBr, of each arm were laterally united by suture; in *Crotalocrinus* (Fig. XCII.) all brachials of an arm are suturally united by projections at the distal margin of each brachial; in *Petalocrinus* (Fig. XCI.) all brachials of an arm except IBr are fused into a single petaloid plate. Compare also *Melocrinus* (Fig. LXXIV.) and *Eucladocrinus* (Fig. LXXI. 4).

Brachials primitively, and pinnulars nearly always, are united by loose suture (compare Fig. XVIII.). The next stage is imperforate articulation. In the final stage, perforate articulation (Fig. XXIII. 1), there is a well-marked transverse fulcral ridge, pierced by the axial canal; the ventral groove comes nearly up to the ridge at this point. On each side of the ventral groove, and often separated by a slight vertical, *i.e.* dorso-ventral, ridge running down to the axial canal, are two depressions, *fossae;* the ventral pair lodges muscle fibres ("muscular fossae"); and the dorsal pair, interarticular ligament ("ligamentar fossae"). Dorsad of the fulcrum is a deep "dorsal fossa," lodging elastic ligament. This type may be modified by the disappearance of the ventral muscles, the increase of the interarticular ligaments and their fossae, and of the vertical ridge separating them, which now passes dorsad of the axial canal, and the concentration of the dorsal ligament in a pit at the end of the vertical ridge (Fig. XXIII. 2). This is called "trifascial articulation." Further increase of the ligamentar fossae and of the vertical ridge, with the disappearance of the dorsal fossa, produces the "bifascial articulation," adapted only for lateral movement (Fig. XXIII. 3). These forms of articulation may be bilaterally symmetrical, but in pinnuliferous brachials the fulcral ridge is skewed, so that on the distal joint-surface the end of the ridge towards the pinnule is moved dorsalwards.

The syzygy (J. Müller, 1841; P. H. Carpenter, 1884; Bather, 1896) is an immovable sutural union between two brachials of a pinnulate arm, accompanied with loss of the pinnule on the hypozygal (compare Fig. XVIII.). Immobility may be effected in various ways. The apposed faces may be smooth (some Pentacrinids), striated (*Uintacrinus*, most Antedonidae), or dotted (some *Actinometrae*); in *Rhizocrinus* a peg projects from the dorsal region of the epizygal into a pit in the hypozygal (Fig. XXIII. 4), and in some Pentacrinids a dorso-ventral ridge on the epizygal fits into the hypozygal (Fig. XXIII. 5). The former type of syzygy facilitates fracture along the suture, and is specially developed in locomotive forms liable to entangle their arms. The latter type appears different in origin and function.

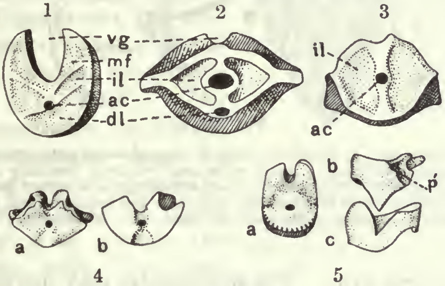


Fig. XXIII.

Arm-joints. 1, brachial of *Isocrinus asteria*, after Joh. Müller. 2, distal face of IBr_1 of *Bathycrinus Aldrichianus* (cf. 6 in Fig. XVIII.), × 8 diam. 3, the same in *Isocrinus Blakei*, × 3½ diam. 4, syzygy of *Rhizocrinus Rawsoni*—*a*, epizygal from its under surface; *b*, hypozygal from its upper surface, × 7½ diam. 5, syzygy of *Isocrinus Blakei*—*a*, upper surface of hypozygal; *b*, epizygal; and *c*, hypozygal in their relative positions, seen from side, × 3½ diam. (2-5 are after P. H. Carpenter.)

ac, axial canal; *dl*, dorsal ligament fossa; *il*, interarticular ligament fossa; *mf*, muscle fossa; *p′*, facet for pinnule; *vg*, ventral groove.

We now return to the extension of the Dorsal Cup. This may be effected, as in *Ichthyocrinus* (Fig. CVIII.), by the direct lateral union of the proximal brachials. At the same time, the proximal ambulacrals enter the tegmen, so that the thecal cavity stretches out further between the actinal and abactinal elements. In many living crinoids the proximal brachials are united by a flexible integument containing minute supplementary plates (*Isocrinus, Calamocrinus*); thus the thecal cavity is enclosed by secondary as well as primary elements. Similar plated membrane may occur between the IIBr or IIIBr of a single arm. The small plates may increase in size and firmly bind together the arms and rami (Fig. XXIV*a*); those between brachia are "interbrachials" (iBr); between IIBr, "intersecundibrachs" (iIIBr), and so on. Similarly there are interambulacrals of various orders; the iIAmb, merging at the sides of the theca into the iBr; the iIIAmb separated by the thecal cavity from iIIBr; the iIIIAmb, and so on. The interbrachials sometimes, though rarely, descend between the radials. Not merely brachials, but also pinnulars may be incorporated in the cup, and between pinnules are developed "interpinnulars" (e.g. *Uintacrinus*, Fig. CIII.); it is often hard to distinguish fixed pinnulars from supplementary plates. Except in primitive forms (*e.g.* Reteocrinidae), the interbrachials have a similar arrangement in each interradius of an individual. Indeed, the arrangement often serves as a means of distinguishing species and genera. This

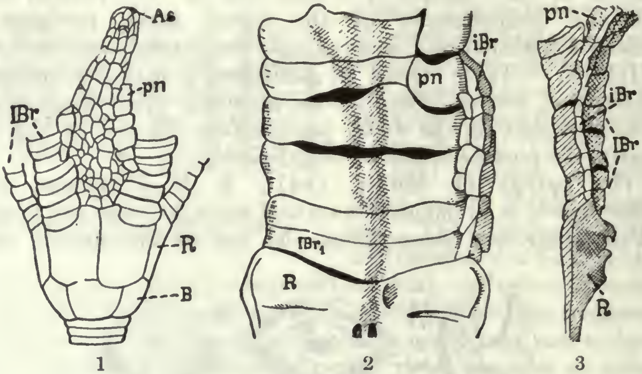


FIG. XXIV.

Calamocrinus diomedeae. 1, posterior view of cup, showing attachment of anal tube to pinnules and proximal brachials, × 4/3; 2, radial and proximal brachials seen from inside of cup, showing attachment of interbrachials (much enlarged); 3, a similar portion seen from the side, showing the interbrachials (unshaded) attached to the brachials and pinnulars (shaded). Enlarged. (All after Al. Agassiz.) *As*, anus; *B*, basal; *IBr*, primibrachs; *iBr*, interbrachials; *pn*, pinnulars.

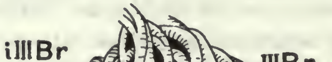


FIG. XXIV*a*.

Sagenocrinus expansus, to show incorporation of arms into cup, by means of secondary plates (these latter are shaded); for lettering see adjoining text. (From Brit. Mus. specimen 57147.) × 2/3.

regularity is, however, often modified in the posterior interradius, which is widened by the insertion of "anal plates," so called because they afford room for the anus, and are continuous with the plates supporting the anal tube when that organ is present.

The Anal Plates of the Camerata appear as a median line splitting the posterior interbrachials, and forming as it were a sixth ray to the cup. They are rarely developed in forms in which the anus is central or comparatively small; a slight enlargement of the posterior calycal elements then sufficed. They are, therefore, regarded as supplementary pieces developed as occasion arose in the position where they are found. The anal tube is an outgrowth of the posterior interambulacrum, and is, in Reteocrinidae, *Glyptocrinus*, and similar forms, supported by a dorsal line of ridged plates continuous with the anals (Fig. XXV.). The ridge is connected with the ridges that unite the posterior basal to the right and left posterior radials, and this indicates that an axial cord passed up it to govern the motions of the tube. In later Camerata, where the interradii and tegmen are less flexible, this differentiation disappears.

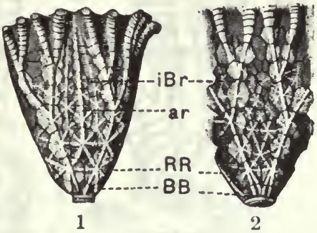
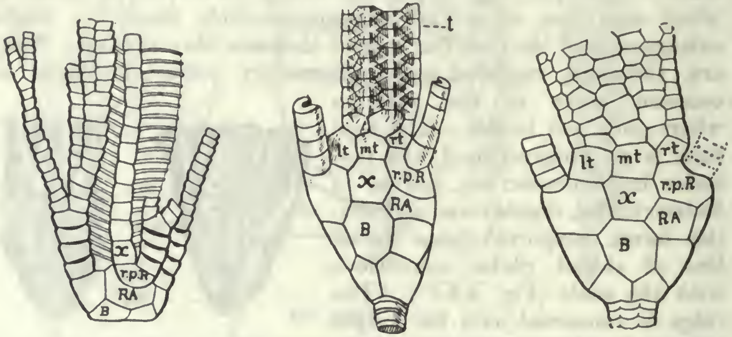


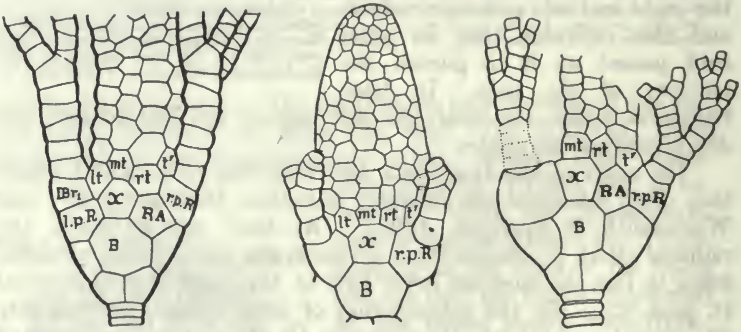
FIG. XXV.

Glyptocrinus decadactylus. 1, from posterior interradius; 2, another interradius. The ridges marking the rays are clearly seen, also *ar*, the anal ridge. (1, after Wachsmuth & Springer. 2, after Meek.)

The anals of the Inadunata and Flexibilia (Fig. XXVI.) have been much discussed (see summary in Bather, 1890 and 1899; and Wachsmuth & Springer, 1897). At least one of them, the radianal (RA), is admittedly a primary, abactinal, radial element, being in fact the modified lower half of the right posterior radial (r. post. R*i*). By the introduction of other plates, and notably one special anal (*x*) into the posterior IR, the r. post. R*s* is pushed to the right, so that RA comes into contact with *x*, and helps in the widening of the area and the support of the anal tube. The theory, originated by Wachsmuth and Springer, that the tube is a modified arm, has since been rejected by them. The less extreme view that the dorsal median line of ossicles supporting the tube represents the proximal left ramus of the right posterior arm, up which the interambulacral peristome around the anus gradually stretched, has the following facts among others in its favour:—The tube is admittedly in close connection with the right posterior ray (Fig. XXVII.); it is up this side that the rectum passes; in *Iocrinus*, *Merocrinus*, and *Castocrinus*, and, to a less extent, in *Heterocrinus*, *Ectenocrinus*, and *Ohiocrinus*, the proximal plate of this median row rests on r. post. R; in *Iocrinus* the articulation between r. post. R and this proximal plate differs from that between r. post. R & IBr_1 only in size (Fig. XXVIII.); in *Iocrinus* the ventral groove of the median series coalesces in r. post. R with the ventral groove of right posterior arm; this, and other evidence from Heterocrinidae, shows that the median anal series was innervated from the axial cord of r. post. R. The only argument



1. *Iocrinus subcrassus.* 2. *Dendrocrinus longidactylus.* 3. *Dendrocrinus Casei.*



4. *Scaphiocrinus elegans.* 5. *Cyathocrinus longimanus,* anal area. 6. *Parisocrinus.*

Fig. XXVI.

Diagrams of the anal area in various Inadunate Crinoids. (From Bather, after Wachsmuth & Springer, Hall, and Angelin.)

against the view, is the improbability of a change of function in the ramus; still the view is not proven.

A distinct question is whether the anal *x*, which frequently occurs in the posterior interradius of the cup, is a secondary element suddenly introduced, as are the anals of Camerata, or whether it is the proximal median plate of the tube (as in *Iocrinus*, Heterocrinidae, etc.), that has gradually sunk down into the cup. Wachsmuth & Springer hold the former view, believing that *x* is homologous with the strictly interradial anal of Camerata, and that the proximal median plate of *Iocrinus* and Heterocrinidae (which they call *t*) is represented in genera with a special anal *x* by a tube-plate (*rt*) on the left shoulder of r. post. R (Fig. XXVI. 2-6); they assert that "in the earlier and simpler forms, the tube consists of only five [vertical] series, one to each interradius, that of the anal side resting upon *t*. Later on, as the tube grew larger, a new row of plates was introduced with plate *x* supporting it. When there are three series [at the posterior side], as in *Dendrocrinus*, the third generally rests upon one side of the left posterior radial. The arrangement of the plates within the rows is so regular, that if a sinking of the plate *t* had taken place, it would certainly be indicated by some disturbance among the lower plates in the tube." In this sentence the proximal median plate *t* (our *x*) of *Heterocrinus* is identified with *rt* of *Dendrocrinus;* but no proof has yet been given that the added series may not be those starting from *rt* and *lt*, rather than from *x* and *lt*. On the other hand, the view that the series *x* is homologous with the series *t*, is supported by the general size and appearance of the two, and by the inferred relations of the axial cords. And the homology of *x* with *t* is supported by the facts that the position of *t* with reference to r. post. Rs, does vary from a higher to a lower level in early genera, while the position of *x* to the adjacent radials likewise varies. In late Carboniferous genera of Dicyclic Inadunata, *x* certainly appears to pass up out of the cup (Fig. XXIX.), and this interpretation is confirmed by the migration of the anal in the development of *Antedon*, which anal is universally homologised with *x* (Fig. XXX.); but if a plate can pass up, it can also pass down, as

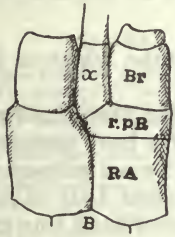


Fig. XXVII.

Anal area of *Heterocrinus isodactylus*, showing close connection of anal (*x*) with right posterior superradial (*r.p.R*). Enlarged. (From Bather.)

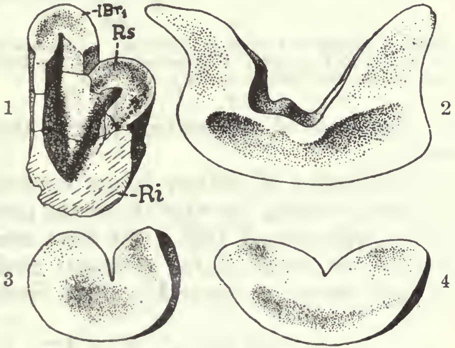


Fig. XXVIII.

Iocrinus, showing connection of anals and brachials. 1, part of the r. posterior ray seen from inside the cup; 2, upper articular surface of *Ri*; the groove on the left goes to *x*, that on the right to brachials; 3, left upper articular surface of *Rs*, supporting *x*; 4, right upper articular surface of *Rs*, supporting IBr_1. Enlarged. (From Bather.)

is further proved by the phylogeny of the Calceocrinidae. The fact that x is wholly or partly in the cup, and t partly or wholly outside, does not make them different morphological elements; for there is now admitted to be no difference between interambulacrals and interbrachials, or between fixed and free brachials. Consequently in this work the symbol x will always be applied to the proximal plate of the median line of the anal tube, whatever its position.

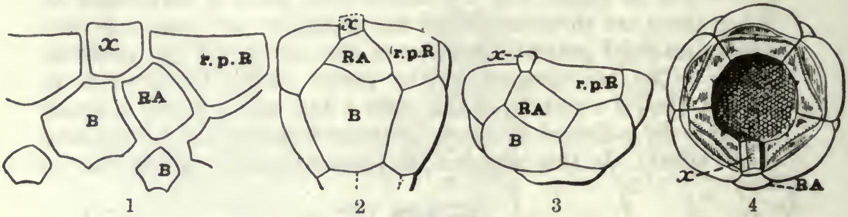


Fig. XXIX.

Upward passage of anal (x) in *Ulocrinus*. 1, anal area of "*Ulocrinus*" *Blairi*; 2, posterior view of *U. Buttsi*; 3 and 4, *U. Kansasensis*, the cup from posterior and from above, × $\frac{2}{3}$. (From Bather, after Miller & Gurley.)

Modification of the cup is not confined to the fixed brachials and interbrachials, but also affects the patina. We have discussed the disappearance of IBB. We have also to note a tendency to fusion in the plates of the proximal circlet, whether IBB or BB, and their change of shape due to the introduction of anals into the patina. The first stage is the fusion of one pair, producing 1 large and 3 small plates (Fig. XXXI. 2). This is almost entirely restricted to monocyclic genera, where the plates that fuse are the right and left anterior basals. Next comes the fusion of two pair, producing 1 small and 2 large plates (Fig. XXXI. 3). This occurs in both Mono- and Di-cyclica. In the former the small plate is the left anterior basal, or rarely left posterior basal; whereas in Eublastoidea it is the right anterior basal (Fig. XXXI. 4). In Dicyclica three infrabasals have been observed only among

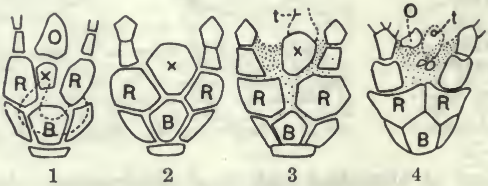


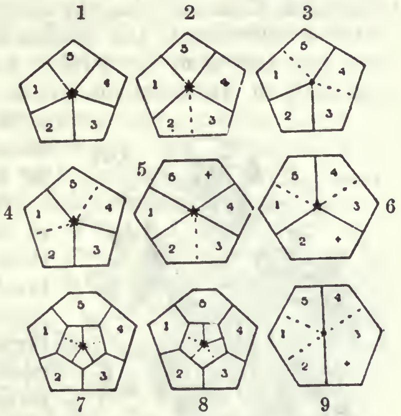
Fig. XXX.

Migration of the anal in *Antedon*. (After W. B. Carpenter and M. Sars.) Originating between *RR*, the plate x gradually moves upwards, eventually atrophying till only two small fragments remain at the base of the anal tube (t). The dotted lines in 1 show the course of the gut. These figures also show change in shape of *RR*, and atrophy of orals (O).

Inadunata and Flexibilia; in the former group the small plate is often, but not always, the anterior infrabasal (Fig. XXXI. 7); in the latter it is (*apud* W. and Sp.) always the right posterior infrabasal (Fig. XXXI. 8). A bipartite base is formed only in a few Monocyclica; the two plates lie on the right and left sides of the cup (Fig. XXXI. 9). Finally, all plates of the proximal circlet may fuse into a solid ring, both in Mono- and Di-cyclica. The infrabasals may fuse with the proximal columnal in Flexibilia, thus forming a pseudomonocyclic type. The basals may be overgrown by, and incorporated with, the radials, as in *Eugeniacrinus.*

The symmetry of the base is modified by the presence of anals. An anal resting on the basal circlet causes one of the basals to double in width, so that the base becomes hexagonal instead of pentagonal. Thus the quadripartite base comes to consist of a posterior and anterior large plate, and two small lateral plates (Fig. XXXI. 5). These tend to approximate in size. In *Xenocrinus* (Fig. LXXVIII.), interbrachials as well as anals come down between the radials, so that the basals are nearly equal in size, but irregular in shape, and make the base decagonal. Removal of anals and interbrachials from the radial circlet leaves a pentagonal quadripartite base, such as is found in Melocrinidae (p. 161). An anal resting on a tripartite base is accompanied by increased width in the small left anterior basal (Fig. XXXI. 6). But in the bipartite base the small basal fuses with the combined posterior and left posterior basals, while the combined right-hand basals increase in width (Fig. XXXI. 9). In most Dicyclica the infrabasals do not assume a hexagonal outline; for the anals do not occur in the basal circlet, but *x* truncates the upper surface of the posterior basal. Exceptions are *Sagenocrinus, Carabocrinus* (Fig. LXXXIV.), *Strophocrinus,* and *Thenarocrinus* (Fig. XCVI.).

FIG. XXXI.



Bases and their modifications. 1-6 and 9, monocyclic; 7 and 8, dicyclic; 1-4, pentagonal, unaffected by anal; 5, 6, 9, hexagonal, affected by anal. In all the anal side is uppermost, and the plates are numbered on Jaekel's plan (see table, p. 110); the imaginary additional piece is marked +. 1, 5 *BB*; 2, 4 *BB*; 3, 3 *BB*, Crinoid type; 4, 3 *BB*, Blastoid type; 5, 4 *BB*; 6, 3 *BB*; 7, 3 *IBB*, as usual in *Dicyclica inadunata;* 8, 3 *IBB*, as usual in *Flexibilia impinnata;* 9, 2 *BB*. (Adapted from Wachsmuth & Springer.)

The enlargement of anal structures was not the only factor in the modification of the typical pentamerism. Allusion need not be made to the (apparently sudden) dropping of a radius to form *Tetracrinus* (p. 153), or the duplication of the radii to form *Promachocrinus* (p. 195), and similar cases. Nor need more be said as to the enlargement of certain radii (e.g. *Pisocrinus*), the bisection of others (e.g. *Heterocrinus*), and so forth, since in these cases the outwardly symmetrical appearance of the cup usually remained unaltered. But certain factors, probably of physical environment, such as currents and direction of food-supply, or possibly connected with locomotion, have at different times produced similar results in different families. A bending over of the cup, accompanied by diminution of certain radials, was common in Eugeniacrinidae, as well shown by Jaekel (1891). In the remarkable Calceocrinidae the crown was bent towards the right posterior interradius, and far-reaching changes brought about in both cup and arms (p. 148). Even in an unattached species, apparently of *Agassizocrinus*, similar growth of one side took place at the expense of the other. These cases are comparable to the irregular Eublastoids.

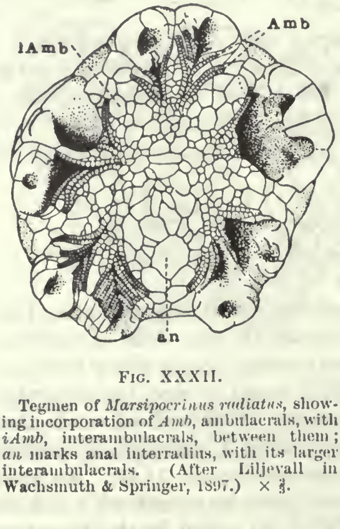


Fig. XXXII.

Tegmen of *Marsipocrinus radiatus*, showing incorporation of *Amb*, ambulacrals, with *iAmb*, interambulacrals, between them; *an* marks anal interradius, with its larger interambulacrals. (After Liljevall in Wachsmuth & Springer, 1897.) × $\frac{2}{3}$.

Concomitant with modifications in the dorsal cup were modifications in the Tegmen. Just as brachials entered the cup, so their covering-plates (Amb) entered the tegmen, prolonging the food-grooves over its surface. And corresponding to interbrachials in the cup, there arose interambulacrals (iAmb) in the tegmen (Fig. XXXII.).

Other changes that took place are difficult to describe without raising the question of the homology of the plates covering the mouth. In *Antedon* five interradial plates (O) are developed before the radials and at the same time as the basals, upon which they rest (Fig. XXXIII. 1). Between these two circlets appear the radials, upon the shoulders of which the five adoral interradials then rest (Fig. XXXIII. 2), forming a pyramid closed over the oral centre, but soon opening at the apex to expose the entrance to the mouth (tentacular vestibule). The posterior of these plates surrounds the hydropore. At a more advanced stage they become separated from the radials by ambulacrals and interambulacrals

(Fig. XXXIII. 5), and finally, in most species of *Antedon*, are resorbed (cf. Fig. XXX. 4). These plates are called *oralia* (O). Their prominence in early stages shows them to be primary elements of the theca, probably well developed in the adult of primitive forms. Five triangular plates that cover the mouth in the recent *Holopus*, *Hyocrinus*, *Rhizocrinus*, and *Thaumatocrinus*, are by all writers homologised with orals (Fig. XXXIV.). In all Antedonidae, *Bathycrinus*, and *Calamocrinus*, they are almost or entirely resorbed in the adult. The ambulacra pass to the mouth between or below the orals.

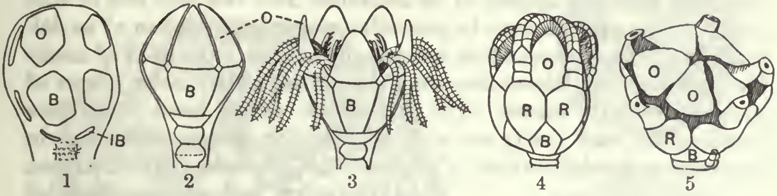


FIG. XXXIII.

Development of orals in *Antedon*. 1 (after Bury), *IB* still visible, no *RR* yet formed. 2 (after Allman), *O* closed; between them and *BB* are the developing *RR*. 3 (after Allman), *O* open, exposing oral tentacles; no arms yet exist. 4 (after W. B. Carpenter), *O* now separated from *BB* by *RR*, which support arms. 5 (after W. B. Carpenter), arms cut off above first brachial so as to show *O*, which now surround the mouth; the shaded portion represents integument, in which ambulacrals and interambulacrals are developed.

Note also gradual decrease in size of *BB*. A further stage in oral history is seen in Fig. XXX. 4, which is from another species.

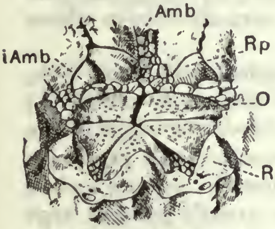


FIG. XXXIV.

Tegmen of *Holopus*. The arms are removed from the side nearest the observer, showing the articular surfaces of *R*, the radials, which are fused together. *Amb*, ambulacrals, which pass down the brachials to the tegmen and a little way up between the orals; *iAmb*, interambulacrals, partly separating brachials from orals; *O*, five perforate orals; *Rp*, processes of fused *RR*. (After P. H. Carpenter, 1888.) × $\frac{5}{2}$.

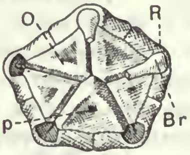


FIG. XXXV.

Tegmen of *Haplocrinus mespiliformis*. *Br*, first brachial; *O*, oral; *p*, pore in post. O; *R*, radial. (After Wachsmuth & Springer, 1888.) × 6.

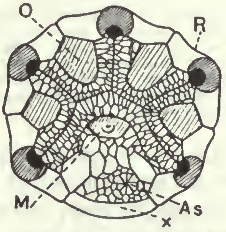


FIG. XXXVI.

Tegmen of *Hybocrinus conicus*. Small irregular ambulacrals overlie the apposed edges of *O*, the orals, which are shaded. Post. *O* has a hydropore, and is therefore a madreporite, *M*. *As*, anus, lies between this and *x*, the anal plate of the cup. *R*, radials, with arm-facets shaded, and nerve channel black. (Based partly on MS. drawings by W. R. Billings. Natural size.)

In *Hybocrinus*, *Haplocrinus*, *Carabocrinus*, and other primitive genera are five interradial plates precisely resembling the orals of the larval *Antedon* in shape and position (Figs. XXXV., XXXVI.).

The generally accepted view that these are orals is confirmed by the frequent presence of a pore or pores in the posterior one, as in larval *Antedon* and adult *Hyocrinus*, and by the situation of the anus between this plate and the adjacent RR; in *Haplocrinus* the pore and the anus appear to be combined near the oral end of this plate. These plates have in preceding pages been spoken of as deltoids (Δ). They meet close around the mouth like the Δ of many Blastoids, and in *Hybocrinus* and *Carabocrinus* they show traces of hydrospires of *Codaster* type. On the other hand, they are homologised, and justly so, with five similar plates that occur in *Coccocrinus*, *Symbathocrinus*, *Pisocrinus*, *Allagecrinus*, *Myrtillocrinus*, some *Platycrini*, and the specimen of *Taxocrinus intermedius* (Fig. XXXVII.) described by Wachsmuth & Springer (Nov. 1888). In most of these genera the orals (or Δ) cover the mouth, and the food-grooves pass in under them; but in *Taxocrinus* the mouth is open, and the grooves with ambulacrals pass between the orals; while in *Hybocrinus* and *Carabocrinus* the ambulacrals rest on the edges of the apposed orals, showing that the grooves were actually above those plates.

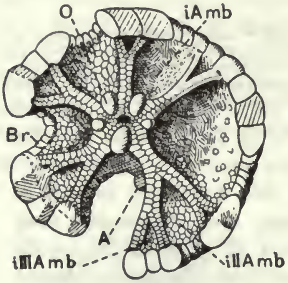


Fig. XXXVII.

Tegmen of *Taxocrinus intermedius*. *A*, anal ridge; *Br*, edges of brachials; *iAmb*, *iIIAmb*, *iIIIAmb*, interambulacrals of first, second, and third order; *O*, five orals a little distance from the peristome. (After Wachsmuth & Springer, 1888.)

From this primitive Palaeozoic type, three lines of evolution start: (1) Ambulacra pass over the edges of the orals, while ambulacrals and sometimes interambulacrals gradually cover the orals, which seem thus to sink below the surface and to diminish in size; the posterior oral, however, usually remains large and is pierced by hydropores, while the increased size of the anal tube pushes it more towards the oral centre (*e.g.* *Euspirocrinus*, *Cyathocrinus*, *Cupressocrinus*, Figs. XXXVIII., XXXIX.). (2) Ambulacra and ambulacrals pass between the orals, leaving an open mouth, while the orals gradually atrophy (*e.g.* *Taxocrinus*, Fig. XXXVII., probably other Palaeozoic Flexibilia, and certainly many of their Neozoic descendants). (3) Ambulacra pass beneath the orals, and gradually also beneath other tegminal plates, which are developed *pari passu* with the incorporation of brachials in the cup, and which thus separate the orals from the periphery of the tegmen (*e.g.* Adunata and Camerata, Fig. XL.; cf. Caryocrinidae, p. 66).

At the same time, in types (1) and (3) a modification of the ambulacrals takes place. The proximal ambulacrals covering the mouth in (1) become large, and assume a pentagonal arrangement simulating that of primitive orals (*e.g. Gissocrinus*, Fig. XLI., *Crotalocrinus*, Fig. XCII.; cf. Eublastoidea). Other ambulacrals, especially axillary Amb, increase in size, and form prominent bosses on the tegmen, called "radial dome-plates" (Fig. XLII.); the effect of this is enhanced by the sinking of the other ambulacrals (*e.g.* Actinocrinidae). These two facts suggest that the proximal dome-plates of Camerata, regarded as orals by Wachsmuth & Springer, and so quoted under head (3), may after all be modified ambulacrals.

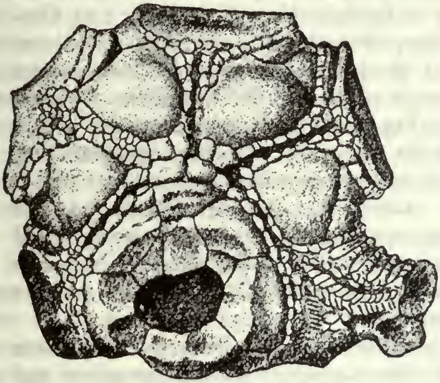


FIG. XXXVIII.

Tegmen of *Euspirocrinus spiralis*, showing four cordiform deltoids or orals, and a madreporite, with ambulacrals overlying their apposed edges. In the posterior interradius is the base of the broken off anal tube. (From Bather, 1893.) × 3.

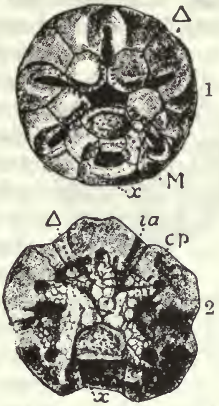


FIG. XXXIX.

Tegmen of *Cyathocrinus*. 1, *C. planus* with ambulacrals and interambulacrals removed, exposing apposed edges of orals (Δ) and madreporite (*M*). 2, *C. mammillaris* with ambulacrals (*cp*) and interambulacrals (*ia*) almost entirely covering orals (Δ) and peristome. (From Bather, 1892.) × 2.

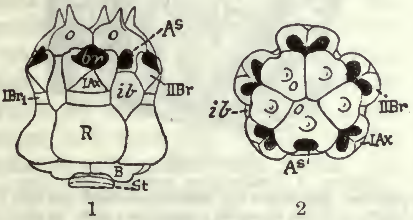


FIG. XL.

Cylicocrinus nodosus, to exemplify the simplest type of Camerate tegmen. 1, from l. post. radius; 2, from above. *As*, anus; *B*, basals; *br*, opening for food-groove and underlying canals; *ib*, large interbrachials (suborals, Jaekel). Other letters as usual. (After Joh. Müller, 1855.) × 2.

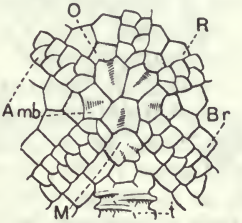


FIG. XLI.

Tegmen of *Gissocrinus arthriticus*, showing ambulacrals (*Amb*) passing down arms and over apposed orals (*O*), and becoming enlarged over peristome. Post. O remains as a folded madreporite; *t*, anal tube. Other letters as usual. (From Brit. Mus. 46457.) × 3.

The most conflicting views have been held from time to time by the same and by different writers as to the homologies of these plates. That here put forward agrees in the main with Neumayr's (1889), but is based on facts not accessible to him. Wachsmuth & Springer (1897) deny the homology of the deltoids in Eublastoidea, *Hybocrinus*, and Cyathocrinidae, with the orals in *Haplocrinus* and *Antedon ;* the plates here regarded as enlarged ambulacrals (*e.g.* in Eublastoidea, Cyathocrinidae, Fig. XLIII., *Crotalocrinus*) are taken by them to be orals, and they imagine that they undergo resorption, fission, and other changes, stating that they are relatively larger in young specimens. As to the origin and homologies of the large interradial plates in Inadunata (here called Δ or O), those authors are undecided.

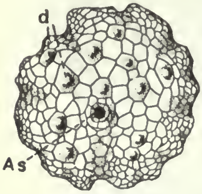


Fig. XLII.

Tegmen of *Megistocrinus nodosus*, showing radial dome-plates, *d*. (After Wachsmuth & Springer, 1897.) × ½.

The gradual sinking of the ambulacra and their covering-plates below not only the orals but other tegminal plates, has given rise in the typical Camerata to structures so differentiated that they were long misunderstood, and their chief elucidator, Wachsmuth, believed in 1877 that the tegmen of Palaeozoic crinoids was "a solid vault or dome," which could not "in the remotest degree be homologised with the soft peristome of" recent crinoids. "It forms," he said, "a part of the abactinal system"; "a continuation of the radial and interradial series of the dorsal side, and serves merely as a covering and protection for the organs underneath." From this it was generally inferred that an originally flexible tegmen ("disc" it was called, as in recent crinoids) had been overgrown by "a free arch which braces the entire oral side of the body without the aid of oral plates" (W. & Sp. 1881). The disc remained as an "inner test," in which were ambulacra and possibly orals. Because of this structure, supposed to obtain to a greater or less extent in all Palaeozoic crinoids, but not in their successors, the Crinoidea were divided into Palaeocrinoidea and Stomatocrinoidea, the latter term being altered by P. H. Carpenter to Neocrinoidea.

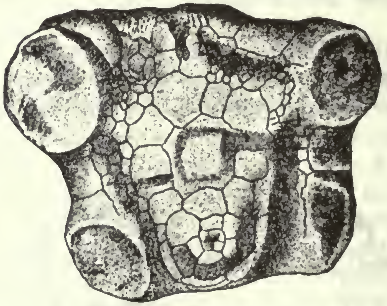


Fig. XLIII.

Tegmen of *Cyathocrinus ramosus*. The large tegminal plates are not homologous with the deltoids, but the squarish central one may be the madreporite. (From Bather, 1893.) × 3.

As fresh facts kept coming to light there was a good deal of shifting of ground and mutual criticism on the part of Wachsmuth & Springer and Carpenter. The supposed difference, and consequently the classification, were rejected by Neumayr (1889) and Bather (1889-90). Independently and synchronously Wachsmuth & Springer (1889) concluded, chiefly on the evidence of *Taxocrinus intermedius* (p. 126), that "in some Palaeozoic crinoids the mouth is exposed, and there is no vault aside of the orals"; also that "all attempts to subdivide the Crinoidea by separating the Palaeozoic from the Mesozoic and later forms as natural divisions will have to be abandoned." But it was not till 1891 that they published their recantation of the view that "the Camerata had a vault and a subtegminal disk."

The explanation of the Camerate tegmen given by Wachsmuth & Springer in 1891 was readily accepted and now prevails. It may be condensed as follows:—The plates of the tegmen were at first small and yielding, as in the Ichthyocrinidae and in most recent crinoids; in this state when the arms are open the ventral surface is depressed, when they are closed it bulges upwards. To afford better protection to the viscera the tegminal plates became more solid; the tegmen being thus less flexible was fixed perforce in its protruded state. The covering-plates of the ambulacra had perhaps been closed from the beginning, but as, through the upswelling of the tegmen, the grooves were now more exposed, further protection was needed. Consequently they were lowered beneath the surface and, starting from the solid orals, interambulacral plates closed in over them. Certain of the covering-plates, however, especially, it would appear, the axillary pieces, which perhaps could not so easily be covered by other plates, became much stouter, and were still exposed on the surface as solid radial dome-plates. In any form highly developed along these lines, *e.g. Cactocrinus* (Fig. XLIV.), the food-grooves, water-vessels, and blood-vessels are sunk right beneath the tegmen, and are enclosed in a tube consisting of alternating ambulacrals above and adambulacrals or side-plates below. The interambulacral plates of the tegmen send curious extensions into the interior of the calyx, and these extensions, spreading out, form what used to be regarded as

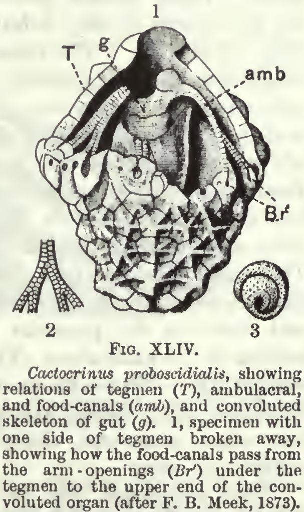


FIG. XLIV.

Cactocrinus proboscidialis, showing relations of tegmen (*T*), ambulacral, and food-canals (*amb*), and convoluted skeleton of gut (*g*). 1, specimen with one side of tegmen broken away, showing how the food-canals pass from the arm-openings (*Br*) under the tegmen to the upper end of the convoluted organ (after F. B. Meek, 1873). × $\frac{3}{2}$. 2, one of the food-canals, from above, further magnified (after Meek). 3, the convoluted organ, from below.

a disc. We may, with Wachsmuth & Springer, regard the extensions as caused by the perforation of the plates for water-canals; or we may regard them as simple processes for the purpose of adding strength, without forgoing lightness, by a system of girders.

The supposition just quoted, as to the existence in Camerata of a complicated water-vascular system, is supported by the connection of the internal passages with small pores near the arm-bases (Fig. XLV.). Such have been observed by Wachsmuth & Springer in Actinocrinidae, Batocrinidae, Rhodocrinidae, and Melocrinidae; they are placed in the cup-wall at the level of the tegmen, between the arms and their rami, and their canals are separated from the subtegminal arm-grooves by a thin partition. In *Batocrinus*, *Strotocrinus*, *Steganocrinus*, *Eucladocrinus*, and others in which the arms branch off alternately, there is a pore to each ramus that springs directly from the dorsal cup. *Dolatocrinus* may have four to six in each interradius, and two to four between each $\overline{\text{IIBr}}$ series. Other genera have only ten pores. In *Gilbertsocrinus* these are at the end of long tubular extensions of the interradial areas (Fig. CXXVII.). The facts are so plain, that the introduction of water into the thecal cavity for aeration of the viscera seems probable; but the connection of these passages with the hydrocoel or with branches thereof is a different question. The pores may possibly have replaced the hydropore or the madreporite of certain Inadunata. In many recent crinoids pores pierce not only the O. but the iAmb, often in great numbers, being least numerous in the posterior IR. *Antedon bifida* (Fig. XLVI.) is said to have 1500. They may also occur on the edge of the theca between the arms. In *Actinometra* they are chiefly developed near the ventral grooves, and even on the pinnules. These pores communicate with the coelom or its extensions (Fig. XLVII.), and so indirectly with the water-ring. Where there are few pores (*e.g. Rhizocrinus*, Fig. X.), a process (stone-canal) stretches out towards each from the ring; but, when numerous, there is no correspondence between stone-canals and pores.

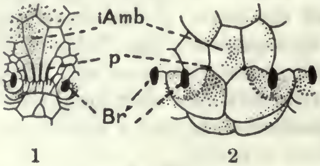


Fig. XLV.

Pores in Camerata. 1, *Dolatocrinus Lyoni*, an interradius, showing slit-like pores (*p*) between interambulacrals (after Wachsmuth & Springer, 1897). Nat. size. 2, *Batocrinus*, showing pores (*p*) between interambulacrals and fixed secundibrachs (from Brit. Mus. specimen 75592). × $\frac{5}{3}$. *Br′*, passage of arm-canals into thecal cavity.

The statement has repeatedly been made (by Trautschold, Lovén, Wachsmuth & Springer) that pores occur on the suture-lines between the plates composing the anal tube of many Inadunata. In the cases to which the last-named authors now restrict the statement, the tube-plates have strong axial folds, being no doubt connected along these by thicker ligament, innervated from the axial cords (Fig. XLVIII.). The depressions between these folds are often deep, and it is in them that the pores are said to lie. It is supposed that such genera have no madreporite, and that the pores aerated the rectum or a blind extension thereof, for the anus often opens low down on the anterior face of the tube. The statement has been definitely disproved for many forms hitherto said to have such pores. But Wachsmuth & Springer (1897, pl. vii., figs. 2*b*, 5, 6, 9) support it by figures which, if correct and correctly interpreted, prove it for some species up to the hilt—and much further. For they show pores not only on the sutures, but penetrating the plates; not only in the interaxial depressions, but on the axial folds; not only in the tube, but in the dorsal cup.

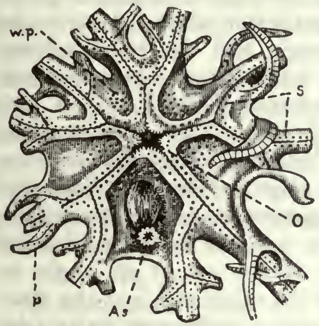


Fig. XLVI.

Ventral surface of *Antedon bifida*, diagrammatised from various authorities. × 4 diam. *As*, anus; *O*, mouth; *p*, pinnules; *s*, sacculi; *w.p*, water-pores.

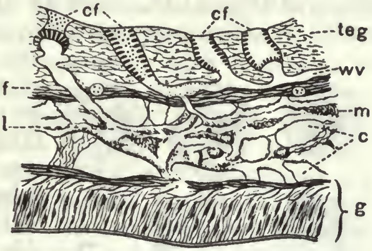


Fig. XLVII.

Vertical section through tegmen and underlying structures of *Antedon bifida*. Shows four pores, with ciliated funnels (*cf*), piercing the integument (*teg*), and communicating by a water-vessel (*wv*) with lacunar vessels (*l*) in the connective tissue of the mesentery (*m*). The funnels are cut through in different directions. *f*, fibrous layer of integument; *c*, coelomic cavities; *g*, gut-wall, showing outer fibrous layer, epithelium, and inner cuticle. (After Vogt & Jung, 1886.) Greatly magnified.

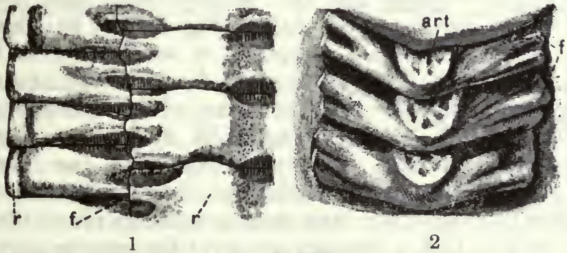


Fig. XLVIII.

Structure of the anal tube in an Inadunate Crinoid, *Mastigocrinus loreus*. 1, plates in normal position, from left edge of distal third of tube; *f*, transverse folds connecting the main axial ridges, *r*. 2, plates from the proximal third, disturbed and exposing the articular facets (*art*) of the axial ridge. (After Bather, 1892.) × 10 diam.

The last organ of which the modifications need be considered is the Stem. The simplest form of columnal (after the fusion of the pentameres) is circular, but with a tendency to pentagonal outline. The joint-surface is radiately striated. The lumen may be large and circular (Fig. XLIX. 1), or small, and circular or five-rayed (Fig. XLIX. 2 and 3). The assumption of a pentagonal outline is often accompanied by a restriction of the striation to the margin and the concentration of the longitudinal ligament-fibres in five bands (Figs. XLIX. 4 and CXI. 7-10). The joint-surfaces may become elliptical, with a fulcral ridge in the long diameter and ligamentar fossae on either side; in this case the long diameter of one end is set at an angle to that of the other end, and the stem thus gets a corkscrew twist (*e.g.* *Platycrinus*, Fig. XLIX. 5), and so can bend in any direction. In a Russian Carboniferous Platycrinoid the columnals are square in section, and the ridges form diagonals at right angles to one another. In Bourgueticrinidae, *Bathycrinus*, and *Rhizocrinus* this form of joint is strongly marked, and the columnals are usually long and dice-box shaped (Fig. XLIX. 7); the length appears in some cases to be produced by fusion of two at a syzygy. The stem of the larval *Antedon* (Fig. XLIX. 8, 9) has ossicles of the *Bourgueticrinus* type and is very flexible. In two genera of distinct origin—*Herpetocrinus* allied to *Heterocrinus*, and *Camptocrinus* allied to *Dichocrinus*—the stem is rolled up round the crown as shown in Fig. LIX.; the cirri are, over the greater part of the stem, confined to two rows along the sides of the ossicles and directed towards the axis of the coil. In *Herpetocrinus* the ossicles become hollowed towards the inside of the coil, and there is a fulcral ridge parallel to this side; strong (muscular ?) ligaments were developed towards the outer margin. The stem could uncoil and the crown be projected. The structure of the columnals in *Camptocrinus* has not been described, but is said to be similar. Wachsmuth & Springer say that such stems are also found among allies of *Poteriocrinus*.

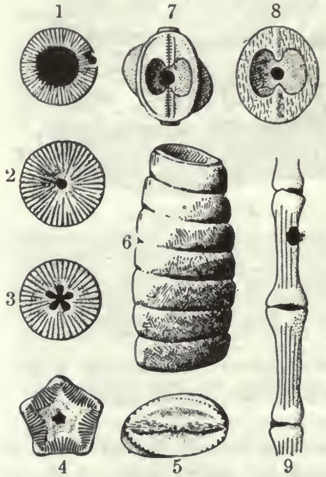


FIG. XLIX.

Types of columnals. 1, *Periechocrinus* (after W. & Sp.); 2, *Actinocrinus* (?), from Brit. Mus. E53; 3, *Actinocrinus*, from Brit. Mus. 38617; 4, Silurian, *genus indet.*, Brit. Mus. 56978, × 2·5; 5, *Platycrinus*, Brit. Mus. 400; 6, *Platycrinus*, showing twist of stem, Brit. Mus. 75906, × ¾; 7, *Rhizocrinus*, from distal region of stem, × 8; 8, *Antedon sarsi*, larva, articular surface of one of the columnals seen from the side in 9 (after M. Sars). Much enlarged.

The axial canal, which in recent crinoids serves to transmit the vascular and nervous prolongations of the chambered organ and axial organ to columnals and cirrals, may in some earlier forms have served other purposes. The lumen is sometimes extraordinarily wide (40 mm. in the root of *Barycrinus*, Fig. XVI. 3). Pores sometimes appear to exist between or through the columnals (*e.g. Barycrinus*, *Crotalocrinus*, Fig. L., *Traumatocrinus*). The distal ends of the cirri sometimes appear to have been open, so that the large axial canal communicated with the sea-water (*e.g. Barycrinus*, *Eucalyptocrinus*, *Cystocrinus*, Fig. L. 2). The flat under surface of encrusting roots is often ridged, as though grooves put the axial canal in connection with the exterior (*e.g. Lichenocrinus*, in which the upper surface is formed of polygonal plates, supported beneath by numerous radiating lamellae). These bases of attachment are, say Miller & Gurley, "as full of pores as sponges." On the theory here adopted as to the origin of the stem, a greater extension of the viscera into it in early forms is probable; the chambered organ itself may have been placed some way down it (compare evolution of siphuncle from visceral cone in Cephalopoda). Assuming that the soft structures contained in the stem-lumen needed aeration, Wachsmuth & Springer have supposed that streams of sea-water entered by these pores. This suggestion seems no more happy than Miller & Gurley's idea that "the mucous or fluid substance, that contained the material for the base, passed through the columnar canal into the pores of the base and was deposited in a softer state than it afterward assumed." We may, however, suppose that these passages served the double purpose of transmitting nutrient fluid to the mesoderm cells depositing the outer layers of stereom as the stem and root grew wider by concentric accretion, and of aerating the same fluid by bringing it near the oxygenated sea-water.

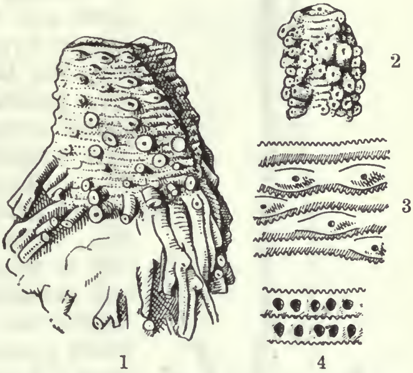


Fig. L.

The development of "pores" from cirri. 1, *Crotalocrinus*, portion of root, with branching cirri below, and attachments of cirri in upper part. These latter show the axial canal that passes from the main axial canal of the stem, through the thickness of the columnals, to each cirrus, and continues to the end of the cirrus. Nat. size. 2, *Cystocrinus tennesseensis*, part of stem, showing stumpy aborted cirri, with axial canals opening at their ends. Nat. size. 3, *Crotalocrinus*, part of stem, showing crenulate sutures between columnals, and on the columnals the atrophied attachments of cirri; compare with the extreme upper part of fig. 1. × 5 diam. 4, *Crotalocrinus*, part of stem, showing total disappearance of cirrus-attachment, and only the axial canals remaining as "pores" piercing the columnals. × 5 diam. (From Bather, 1898.)

In some genera, and especially, as Jaekel has suggested, in those exposed to rough water or currents, the stem shortened considerably while its attachment was preserved (*e.g.* Eugeniacrinidae, Fig. CXX., *Cupressocrinus*). *Cotylederma*, *Eudesicrinus*, and *Cyathidium* are fossil genera, *Holopus* (Fig. CXXI.), a recent genus, in all which the stem is reduced to a mere mass of stereom cementing the cup to some solid object.

Although the Crinoidea are the Echinoderms in which the Pelmatozoan habit has had most effect on the anatomy, yet they present a constant tendency to relinquish the attached mode of life and to lose that typical organ, the stem. So early as the Ordovician, stems are found that during the life of the animal were separated from the root, and became attached to other objects, either by the remaining cirri, or by winding around them. Often the distal end of the stem formed a coiled support like a serpent's tail (*e.g. Acanthocrinus rex*, Jaekel, 1895). In some Silurian genera (*e.g. Calceocrinus*, *Mastigocrinus*) stems have been described that were rounded off at the distal end during life. In *Herpetocrinus* the stem was rarely if ever attached by anything except its cirri; while in the species described by Hall as *Brachiocrinus nodosarius*, the stem ends distally in a bulb. In the Devonian *Myrtillocrinus* the stem ended in a four-fluked grapnel (= *Ancyrocrinus*, Fig. LI.). Similar detachment took place in many Carboniferous and Mesozoic crinoids; the recent *Isocrinus* (= *Pentacrinus*) is known to change its place, probably by swimming with its arms, and the lower surface of the distal columnal is "smoothed and rounded" (Wyville Thomson, 1873).

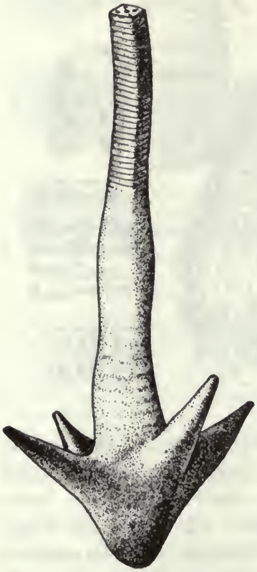


FIG. LI.
Grapnel of *Myrtillocrinus* (after Hall).

Addiction to this habit led to the gradual shortening of the stem; in *Millericrinus Pratti* all stages have been described by P. H. Carpenter (1882), from a stem of seventy columnals over 50 mm. long, down to a single ossicle, the proximale (Fig. LII.). Continuance of this process led to the evolution, along many different lines, of crinoids that are generally described as unstalked, and for which older writers were wont to erect an order, Astylida. These fall into three groups: First, those in which a portion of the stem remains, becoming compressed and fused, with or without the infrabasals, into a cirrus-bearing compound ossicle, to which the term "centro-dorsal" was originally applied, and to which it must be restricted (*e.g. Antedon, Eudiocrinus, Thaumatocrinus*; see Figs. CXVII.-CXIX.). These forms anchor themselves by their cirri, and though capable of crawling, climbing, and swimming, do not often exercise their faculty of locomotion. Secondly, the group in which either a portion of remaining stem, or the lower part of the cup (*i.e.* BB or IBB), becomes solidified, usually by additional deposition of stereom, into a knob, which, one may suppose, serves as ballast or as a sea-anchor; such forms are *Agassizocrinus* (p. 181), *Edriocrinus* (Fig. CXII.), and *Millericrinus Pratti* (Fig. LII.). Both of these groups have a small calycal cavity with thick walls, and there can be little doubt but that all are attached by a stem in the earlier stages of ontogeny. The third group, comprising *Marsupites* (Fig. CIV.), *Saccocoma* (Fig. LXVIII.), and *Uintacrinus* (Fig. CIII.), has no trace of a stem or of any anchoring structure, but is in all respects adapted for free locomotion; the calycal cavity is large in proportion to the thickness of the arms, and is enclosed by thin flexible walls. Of these three genera, *Saccocoma* is the most specialised, and is supposed by Jaekel (1893) to have been pelagic, living in swarms. *Uintacrinus*, with its extraordinarily long and movable arms, may also have been pelagic. The genera of this third group, although of origin as diverse as those in the other groups, resemble one another in the presence of a central, pentagonal, apical plate. This in *Saccocoma* may be the fused basals; in *Uintacrinus* and *Marsupites* it represents neither basals nor infrabasals, but may be the proximale, or the supposed distal columnar plate ("dorso-central"), or a new supplementary plate. It is safest to call it *centrale*.

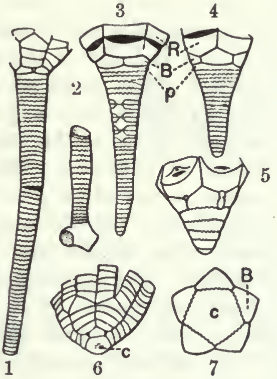


FIG. LII.

Stages in the loss of the stem by *Millericrinus Pratti*. 1, cup with stem of seventy columnals (× $\frac{3}{4}$). 2, distal end of a stem, with apparent root (natural size). 3, cup with fairly long stem, with intercalated new columnals (natural size). 4, cup with stem of twenty columnals (× $\frac{3}{2}$). 5, cup with stem of five columnals (× $\frac{3}{2}$). 6, lower part of crown, with stem reduced to a pentagonal plate (*c*), with slight trace of atrophied next columnal (× $\frac{1}{2}$). 7, base, closed below by a single plate (*c*), with no trace of lumen or of other columnals. This plate is the proximale (*p* of 3 and 4), but is covered by secondary stereom (× 2). (All after P. H. Carpenter.)

Another curious modification, perhaps connected with a free-floating existence, was presented by the root of *Scyphocrinus*. This swelled out into a hollow, chambered, balloon-like body, referred by Barrande to an independent class of Echinoderms under the name *Lobolithus*, and described by Hall as a float, which he called *Camarocrinus*.

As regards the internal organs of the crinoid not much can be said. The most remarkable modifications are those affecting the Gut. In most recent crinoids this makes a simple dextral coil around the thecal cavity, from central mouth to eccentric anus. The mouth may be slightly shifted anteriorly by increase in size of the anus, or by the anal tube coming to occupy the centre of the tegmen, as in *Batocrinus*, or even to pass beyond it towards the anterior margin, as in *Siphonocrinus* (p. 199). But the mouth remains in the axis of the coil, and such forms are called "endocyclic." In *Actinometra* (p. 196) the gut winds in the same way, but instead of issuing immediately the first coil is completed, it continues to coil, not however around the axis of the mouth but around the axis of the anus. The mouth, with its annular accompaniments, therefore lies between the outer coil and the next one, and not in the axis of the coil; such a form is called "exocyclic." This type of coiling does not correspond to the two coils of the echinoid gut, since those are formed by a loop returning on itself, in the way that any tube or cord fixed at the extremities is necessarily lengthened. The coil of the gut in *Actinometra* is therefore doubly peculiar. Yet in the number of its coils it finds a parallel among the Camerata. In many of these (*e.g. Teleiocrinus, Cactocrinus, Batocrinus, Strotocrinus, Macrocrinus, Eutrochocrinus, Habrocrinus*, and *Dimerocrinus*) the gut seems to have been supported by a loose, spicular calcification of the connective tissue around the axial sinus, forming a "convoluted organ" not unlike the shell of *Bulla* (Fig. XLIV. 3). Probably the oesophagus passed down the hollow axis, then the gut coiled dextrally in a widening spire, and the rectum passed up outside, often along a thickened rim. The number of coils was at least three in a *Batocrinus* figured by Wachsmuth and Springer (1897, pl. v. fig. 6). It is remarkable that two of their figures (*ib.* figs. 5 and 7), if correctly described, show a sinistral coil. There is no reason to suppose that the coil of the gut was ever other than dextral in any class or order of Echinoderma, though Jaekel (1897) has made an unconvincing attempt to prove that it was sinistral in Camerata, Cystidea, and Blastoidea.

In *Bathycrinus, Rhizocrinus*, and the larval *Antedon*, the mid-gut, at the bottom of the thecal cavity, is widened into a stomach. In *Bathycrinus* and *Rhizocrinus* are also interradial diverticula from the outer side of the coil, supported by processes from the brachials (Fig. LIII.). Such diverticula were present in the Silurian *Habrocrinus*, if the evidence of the convoluted organ and of Angelin (1878, pl. xxvi. f. 12) can be relied on. In *Pentacrinus* and Antedonidae, and to a less extent in *Bathycrinus*, the gut-wall on the inner side of the coil is thrown into folds or villi (Fig. LIV.). In *Actinometra*, however, with its long coil, such plication is slight.

Sacculi (Fig. LV.) are structures confined to this class. They are globular sacs surrounded by mesoderm, but lying close beneath the epithelium, usually of the external surface. The lower wall of each sacculus is clothed with rather large nucleated cells, apparently derived from mesoderm, and from these grow up processes filled with refringent granules of albuminoid substance. Each process elongates and becomes attached to the upper (*i.e.* outer) wall of the sacculus by a filament. The granular portion of the cell may then separate from the nucleated base, and finally may burst, setting free the granules. These granules, colourless in life, are stained on death by the yellow pigment of the perisome, and show strong affinity for most staining reagents. The sacculi occur chiefly at the edges of the food-grooves; and the side-plates, when highly developed, are notched for their reception (as seen in Fig. IX. 2). They have also been observed in the walls of the gut, in the mesenteries, and above the chambered organ. They are developed so soon as the larva begins to feed. Sacculi have been regarded as calcigenous glands (Wyville Thomson), mucous glands (Bury), excretory organs (Ludwig), symbiotic algae, "Zooxanthellae" (Vogt & Jung), and accumulations of reserve material (Walther, and especially Cuénot, 1891). Since the comprehensive account by the last-named, little has been written on the subject, and his view has found general favour. Sacculi occur in *Antedon*, *Promachocrinus*, *Eudiocrinus*, *Atelecrinus*, *Rhizocrinus*, *Bathycrinus*, and *Pentacrinus*; they are certainly absent from *Actinometra*, and probably from all other recent genera. This fact renders their occurrence of taxonomic value.

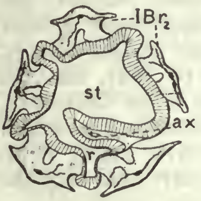


FIG. LIII.

Section across the thecal cavity of *Bathycrinus Aldrichianus*, at the level of second primibrachs, showing interradial processes of stomach (*st*), the rectum (*r*), and the axial organ (*ax*). (Diagrammatised from P. H. Carpenter.) × 7 diam.

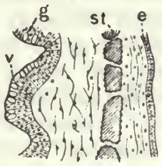


FIG. LIV.

Longitudinal section of wall of anal tube of *Antedon bifida*, showing villi (*v*) of rectal wall and their gland cells (*g*). In the connective tissue layer are plates of stereom (*st*), and outside is epithelium (*e*). (Diagrammatised from Hamann.) Greatly magnified.

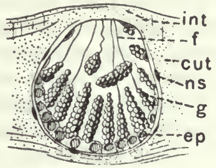


FIG. LV.

Section of a nearly ripe sacculus of *Antedon bifida*. *int*, superficial layer of integument; *f*, fibrillar attachments of contained cells to integument; *cut*, cutis surrounding sacculus, and containing nuclei (*ns*); *g*, granular masses of the contained cells; the large nuclei of these cells are seen below in the lining epithelium (*ep*) of the sacculus. (After Cuénot.) × 200 diam.

THE CLASSIFICATION OF THE CRINOIDEA.

When the modifications above described have been grasped, when it is remembered that these are only the more usual among the changes that take place, and that there are others even more remarkable, and when it is learned that most of these may affect members of any group at any period, then it will be understood that the decipherment of the few and fragmentary leaves of crinoid history that have been preserved to us has been a long and difficult task, full of vain attempt and rejected theory, and that classification after classification has been raised but to fall; and still the leading writers cannot agree, even provisionally.

An admirable account of the literature on this class, from Agricola, in 1558, to C. F. Roemer, in 1853, was given by de Koninck and Le Hon (1854), and supplemented by W. B. Carpenter (1866). The nomenclature of genera and species dates, of course, from 1758, the year of publication of the tenth edition of Linnaeus's *Systema Naturae;* but neither Linnaeus nor his immediate successors were more happy in their dealings with this then little known group than more ancient authors. It was J. S. Miller of Dantzig and Bristol, who, in 1821, laid the foundation for a scientific knowledge and classification of the CRINOIDEA, as he was the first to name them. Accounts of the subsequent growth of knowledge and theory are so accessible in Zittel (1879, 1899), P. H. Carpenter (1884), and Wachsmuth and Springer (1897), that only the main stages need recalling, and that briefly.

Miller's CRINOIDEA excludes unstalked genera; the others known to him are divided into :—ARTICULATA : ossicula forming the cup articulating, *Apiocrinus, Pentacrinus, Encrinus.* SEMI-ARTICULATA : plates of cup articulating imperfectly, *Poteriocrinus.* INARTICULATA : plates adhering by sutures, lined by muscular integument, *Cyathocrinus, Actinocrinus, Rhodocrinus, Platycrinus.* COADUNATA : proximal ossicles of cup anchylosed to proximal columnal, *Eugeniacrinus.* The principles of classification here adopted profoundly influenced subsequent attempts, while the genera form the types of modern families.

Joh. Müller (1843) meant by "Crinoidea" all Pelmatozoa, distinguishing the crinoids proper as *Crinoidea brachiata.* Among these he retained Miller's ARTICULATA, adding to it the Antedonidae, and stating that the rays developed from the base of the cup, and merged into the free arms; that the proximal plates of the rays were laterally united by an integument continuous with that of the ventral surface; that the radial and first primibrach, the primaxil and first secundibrach, were joined by muscles, but the first and second primibrachs by muscles or syzygy; and that food-grooves, mouth, and anus were visible on the tegmen. The peculiar genus *Saccocoma,* unknown to Miller, was made the type of the COSTATA : stemless, without centrodorsal, and with processes from the brachials (*pinnulae oppositae,* Müller). *Haplocrinus mespiliformis* was separated under the head TESTACEA : cup and tegmen forming a firm, connected test, with five ambulacra running up to the mouth. *Holopus* was regarded as an entirely independent and peculiar division of the Crinoidea (*sensu lato*), on account of its sessile cup and the supposed absence of an anus; but no group name was proposed. All other crinoids then known were placed in the TESSELLATA, which included the unstalked *Marsupites;* their cup was said to be composed entirely of plates, to which names were given (BB, RR, Ax, etc.), and their tegmen was said to be solid, with only one opening, and with no food-grooves. This classification, while retaining as a guide the mode of union of the plates, took also into consideration the structure of the tegmen.

Zittel (1879) divided the Crinoidea brachiata, EUCRINOIDEA, as he called them, into three sub-orders, on the basis of Müller's classification, but merging *Holopus* and the Testacea in the Articulata. TESSELATA: cup-plates thin, immovably united by simple suture; tegmen solidly plated; mouth subtegminal; *Marsupites*, *Uintacrinus*, and all Palaeozoic crinoids. ARTICULATA: cup-plates usually very thick, united by articulating or plane sutures; tegmen integumentary, rarely plated, with open food-grooves and central mouth; all Neozoic forms, except those here mentioned under other sub-orders. COSTATA: *Saccocoma* (see under Müller). By this time several families had been founded, notably by C. F. Roemer (1855) and Angelin (1878). These were added to by Zittel, and those of the Tesselata arranged in groups, chiefly according to the construction of the tegmen. Most of the families were well founded, but the characters of the Tesselata and Articulata, though applicable to a few genera, were not really capable of extension to all the forms that had become known since the time of Müller.

Wachsmuth's establishment of the PALAEOCRINOIDEA in 1877, "to include those forms in which the disc is roofed by a second integument, which he supposed to exist in all Palaeozoic crinoids" (W. & Sp.), has already been noticed. The order covered nearly the same ground as the Tessellata, and opposed to it was the order Stomatocrinoidea or NEOCRINOIDEA, corresponding roughly to the Articulata. Carpenter & Etheridge (1881) accepted the division, but laid more stress on the asymmetry of the posterior interradius in Palaeocrinoidea, and therefore suggested IRREGULARIA and REGULARIA.

Wachsmuth & Springer (1885) divided their Palaeocrinoidea into three sub-orders, originally suggested by Wachsmuth's study of the tegmen. CAMERATA: tegmen rigid, formed of rather large thick plates; brachia in part rigidly incorporated in cup by means of interbrachials; Reteocrinidae, Rhodocrinidae, Thysanocrinidae, Glyptasteridae, Melocrinidae, Actinocrinidae, Platycrinidae, Hexacrinidae, Eucalyptocrinidae, Barrandeocrinidae, and Acrocrinidae. ARTICULATA: tegmen flexible, formed of minute plates; brachia may or may not be partly incorporated in cup, but not rigidly; Ichthyocrinidae, Crotalocrinidae.[1] INADUNATA: brachia not incorporated in cup. These were divided into LARVIFORMIA: tegmen of few plates; "disc" covered by "vault"; Haplocrinidae. Cupressocrinidae, Gasterocomidae,[2] Stephanocrinidae; and FISTULATA: "disc" not entirely covered by "vault," but passes out as a porous "ventral sac"; Hybocrinidae, Heterocrinidae, Anomalocrinidae, Belemnocrinidae, Cyathocrinidae, Calceocrinidae, Catillocrinidae, Poteriocrinidae, Encrinidae, Astylocrinidae.

---

[1] Removed to Camerata in 1888.

[2] Removed to Fistulata in 1890.

It must always have been obvious that the Neocrinoidea were a polyphyletic group derived from the Palaeocrinoidea ; the difficulty has been to trace the relationship. This task, however, was forced upon us when those orders were finally rejected. Since that rejection did not carry with it the overthrow of Wachsmuth and Springer's sub-orders, the practical result was the raising of them to the rank of orders, in which Neozoic crinoids had to be appropriately placed.

P. H. Carpenter (1889) referred all Neozoic crinoids to the Articulata (W. and Sp.) as a sub-order, PINNATA, with pinnules ; while the Ichthyocrinidae constituted a sub-order, IMPINNATA, without pinnules. This had the advantage of making Articulata, W. & Sp., very nearly the same as Articulata, Müller. But there is reason to believe that the Pentacrinidae are descended directly from the dicyclic Inadunata ; and since *Pentacrinus* (*i.e. Isocrinus*) was Müller's type, one can hardly escape confusion in using the term Articulata for a group that excludes the Pentacrinidae. FLEXIBILIA, Zittel (1895), is superior and prior to Wachsmuth & Springer's proposed substitute ARTICULOSA (1897), which, moreover, was used in a different sense by Jaekel (1894).

One reason for the above reference of the Pentacrinidae is the discovery by Wachsmuth & Springer (1897) that in the Flexibilia the top columnal is not the latest formed, but a persistent proximale, usually fused with the infrabasals ; whereas in Pentacrinidae, as in Camerata and Inadunata, the top columnal is merely the latest formed, and continually moves from its proximal position as new columnals develop. This, along with the other characters, seems to confirm the independent nature of the order Flexibilia ; at the same time, the resemblance of early genera to contemporaneous Inadunata is so striking, that one must suppose the Flexibilia Impinnata to be derived from non-pinnulate dicyclic Inadunata. Then the want of links between Impinnata and Pinnata suggests that the process may have been repeated, and that Pinnata were derived from Triassic pinnulate Inadunata (Fistulata, W. & Sp.). Whether the mode of stem-growth indicates affinity or parallel modification is a point that demands investigation.

The Larviformia of Wachsmuth & Springer are generally accepted as the most primitive Crinoidea, and as representing the ancestral type of all the orders. On this ground the group might be retained, not as a sub-order of Inadunata, but as an *Urgruppe*, or an independent order (Zittel, 1895). But their geological age forbids us to regard the known genera and species as themselves ancestral to far older forms. If then they be placed with other Inadunata, the question arises whether the distinction of the dicyclic and monocyclic base is not more fundamental than the varying development of the tegmen. A complex tegmen is a development from a simple one, but between dicyclic and monocyclic the barrier runs back to archaean ignorance (Bather, 1893).

The Camerata, like the Flexibilia, form an order fairly well defined on a morphological basis. But here too there are grounds for suggesting that the modifications may have occurred more than once. The evolution of pinnules, of biserial arms, of fixed brachials, interbrachials, and the like, even of a solid tegmen, may all be traced among Inadunata (*e.g.*

Botryocrinus, *Encrinus*, *Uintacrinus*, *Crotalocrinus*, *Cyathocrinus*). The Reteocrinidae (W. & Sp.) present us with the Articulate or Flexible stage of the Camerata, and include both Dicyclica and Monocyclica. It is reasonable to suppose that the monocyclic Melocrinidae, Calyptocrinidae, Batocrinidae, and Actinocrinidae were derived from monocyclic ancestors, whether Reteocrinidae or others, and that the dicyclic Thysanocrinidae and Rhodocrinidae were derived from dicyclic Reteocrinidae and similar forms. On the other hand, the Platycrinidae, and their descendants, Hexacrinidae and Acrocrinidae, are closer to the Inadunata, and sprang probably from monocyclic genera, independently and at a later period. The Crotalocrinidae, which Wachsmuth and Springer now place in the Camerata, are at any rate of totally different origin from all other Camerata, and are intimately allied to *Cyathocrinus* and *Gissocrinus* among the dicyclic Inadunata.

Previous authors have attempted to make their classification serve as a key to structure rather than as an epitome of descent. And the above considerations suggest that Wachsmuth & Springer's system, though far the best from an anatomical standpoint, is not the phylogenetic classification sought by the modern biologist.

A bold attempt at a phylogenetic classification is shortly to be brought out by Jaekel. From his preliminary notice (1894) and subsequent writings it appears that he separates the Camerata (W. & Sp.), under the name CLADOIDEA, from the rest, to which he restricts the name CRINOIDEA. The Crinoidea have radials, five arms with brachials, and ramuli (Jaekel, *supra*), and anal plates connected with right posterior radial; their origin is from such a simple type as has been described above. The Cladoidea originated independently from a many-plated cystid, in which numerous arms produced as many rows of supporting plates (*costalia*) in the cup, not homologous with radials and brachials; the free costalia bear pinnulae (Jaekel, *supra*). The resemblances between Cladoidea and Crinoidea are admittedly great, but all to be explained comfortably by homoplasy and convergence. The Crinoidea (Jaekel) are divided into:—FISTULATA: the root-group, with primitive, simple calyx; including the generally accepted genera, also *Porocrinus*, Crotalocrinidae, and *Marsupites*. LARVATA: essentially the same as Larviformia (W. & Sp.), but supposed to be derived from Fistulata, perhaps through Heterocrinidae. COSTATA: "arms give off undivided, alternating side-branches, serving in part for reception of gonads; cup usually thin-walled and spacious, composed of a circlet of large RR and a tripartite or fused base. No anal plates or tube; tegmen simple, of five O, to which *suboralia*[1] may be added"; Hybocrinidae, Hapalocrinidae, Plicatocrinidae, Hyocrinidae, Saccocomidae, Rhizocrinidae (?). ARTICULOSA: the old Articulata, W. & Sp. *non* Müller; Lecanocrinidae, Ichthyocrinidae, Taxocrinidae. ARTICULATA, Müller *non* W. & Sp.: derived from Fistulata not from Articulosa; Encrinidae, Pentacrinidae, Apiocrinidae, Eugeniacrinidae, Antedonidae. Jaekel's proposals are here alluded to in order that the student may understand the terms used in his forthcoming finely illustrated work. They are valuable as suggesting research for a large amount of confirmatory evidence.

[1] "*Die Oralia mit den Radialien verbindenden Plättchen.*"

The **Classification here adopted** keeps accepted terms so far as possible, but the distribution of the groups is very different from that hitherto accepted. Dividing all Crinoidea into Monocyclica and Dicyclica, we trace in each order a gradual and to some extent parallel modification, here and there diverging in somewhat similar directions. Thus the simplest forms in each order are Inadunata, with free distinct arms, and pass from a Larviform stage, with simple tegmen, to a Fistulate stage, with more complex anal tube and tegmen. At an early period (? Cambrian) in the history of the Monocyclica, the Camerate modification, viz. rigid incorporation of brachials in cup and ambulacrals in tegmen, affected a few forms, and thus arose Monocyclica Camerata. At a later period (Silurian) was a repetition of this modification, but one affecting the cup to a far less extent, and resulting chiefly in a solid tegmen and biserial arms; thus arose the Monocyclica Adunata (or Platycrinoidea), which even Wachsmuth and Springer find a difficulty in placing with the Camerata. These two highly specialised branches died out before the close of the Palaeozoic epoch, the Adunata outliving the Camerata; but the simpler Inadunate forms continued, and reached a high degree of specialisation in their Jurassic descendants, to which the living *Hyocrinus* is closely related. The Dicyclica Inadunata similarly gave off the Dicyclica Camerata, which persisted only a little less long than their monocyclic convergents. The dicyclic Crotalocrinidae of the Silurian are curiously parallel to the Monocyclica Adunata, but it is not worth while to separate them from the typical Inadunata. About the same time arose among the Dicyclic Inadunata the modification that resulted in the Flexibilia, with brachials loosely incorporated in dorsal cup. The

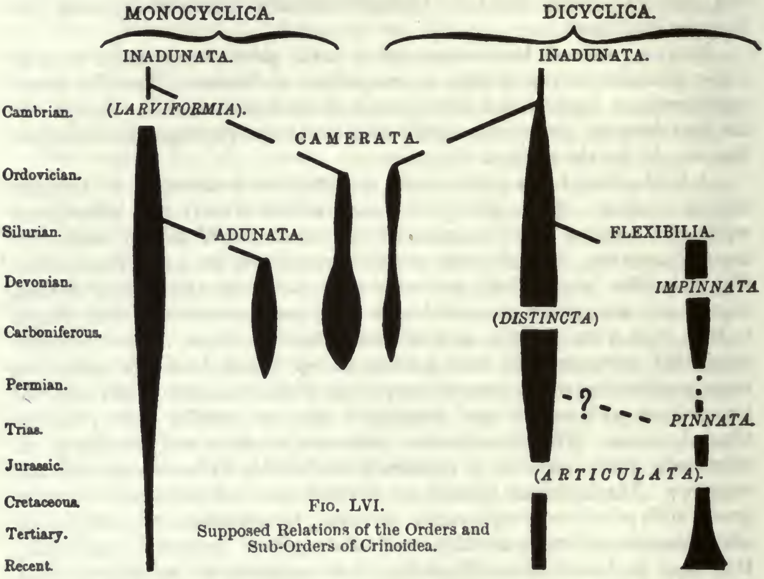

MONOCYCLICA.
DICYCLICA.
INADUNATA.
INADUNATA.
Cambrian.
(LARVIFORMIA).
CAMERATA.
Ordovician.
Silurian.
ADUNATA.
FLEXIBILIA.
Devonian.
IMPINNATA.
Carboniferous.
(DISTINCTA)
Permian.
?
Trias.
PINNATA.
Jurassic.
(ARTICULATA).
Cretaceous.
Tertiary.
Recent.

Fig. LVI.
Supposed Relations of the Orders and Sub-Orders of Crinoidea.

Dicyclic Inadunata came to their acme in Carboniferous times, and only those forms persisted to Neozoic and Recent periods which assumed an Articulate modification, viz. a loose lateral union of proximal brachials, as seen in Pentacrinidae, which are convergents of the Neozoic Flexibilia. The latter sub-order was represented during Palaeozoic times by the Ichthyocrinoidea (Impinnata); between them and the Neozoic Apiocrinidae, Bourgueticrinidae, etc. (Pinnata), the links are missing, but may yet be found among Permian and Triassic crinoids (cf. p. 140). At any rate, the Neozoic Flexibilia, when they assumed the free-swimming habit, took a new lease of life and have their acme in our own day.

The systematic account of the Crinoidea may be prefaced by a table of the **terms** and **symbols** employed in technical description, as explained for the most part in the preceding pages.

PLATES OF PATINA		*See page*	112
Infrabasal	IB	,,	99
Basal	B	,,	99
Superbasal	SB	,,	159
Radial	R	,,	99
Inferradial	R*i*	,,	112
Superradial	R*s*	,,	112
Radianal	RA	,,	119
Pararadial	PR	,,	150
BRACHIALS	free, Br; fixed, $\overline{\mathrm{Br}}$	,,	100, 112
Primibrachs	,, IBr ,, $\overline{\mathrm{IBr}}$	,,	114
First primibrach	IBr$_1$	,,	115
Second primibrach	IBr$_2$	,,	115
Primaxil	IAx	,,	114
Secundibrachs	,, IIBr ,, $\overline{\mathrm{IIBr}}$	,,	114
Secundaxil	IIAx	,,	114
Tertibrachs	IIIBr	,,	114
Quartibrachs	IVBr	,,	114
and so on to the			
Finials	F	,,	115
AMBULACRALS	Amb or c.p.	,,	100, 115
Primambulacs	IAmb	,,	115
Secundambulacs	IIAmb	,,	115
and so on.			
INTERRADIAL AND SUPPLEMENTARY ELEMENTS		,,	109
An interradius	IR	,,	20
Interbrachials	iBr	,,	118
Intersecundibrachs	iIIBr	,,	118
and so on.			
Special anal plate (or proximal median plate of anal tube)	*x*	,,	119
Proximal tube-plate on right	*rt*	,,	121
Corresponding plate on left	*lt*	,,	121
Deltoids	Δ	,,	100
here regarded as homologous with			
Orals	O	,,	124
Interambulacrals	iAmb	,,	118
Interprimambulacs	iIAmb	,,	118
Intersecundambulacs	iIIAmb	,,	118

The various radii and interradii are denoted as explained in the table on p. 110.

We now proceed to review the sub-classes, orders, and families of Crinoidea.

SUB-CLASS 1. MONOCYCLICA, Bather (1899).

Crinoidea in which the base consists of BB only, the aboral prolongations of the chambered organ being interradial; new columnals are introduced at the extreme proximal end of the stem.

ORDER 1. **Monocyclica Inadunata**

(= INADUNATA, W. & Sp. *pars, emend.*)

Monocyclica in which the dorsal cup is confined to the patina and occasional intercalated anals; such Amb or iAmb as enter the tegmen remain supra-tegminal and not rigidly united.

Thirty-one genera are here referred to this order. Of these, 20 diverge from the normal symmetry to a greater extent than by the introduction of anals, viz. 10 through the horizontal bisection of certain RR, other than r. post. R, usually r. and l. ant. RR, while the remaining RR often increase in width; 8 through such increase in width of certain RR (usually l. post. R and ant. R), often accompanied by variation in the number of arms directly springing from RR; 1 by disappearance of a radial (an occurrence also found in some of the other genera), and apparent increase in number of arms springing from RR (as in some other genera). Only 2 of the genera have regularly pinnulate arms, and in 15 the arms are unbranched. In 14, O are not separated from one another or from RR; 11 at least have no anal tube, while in 6 of those the anus if it existed must have pierced post. O. In the rest the anal tube was always supported by a well-defined median ridge of plates, simulating Br. In Dicyclica Inadunata such characters as these are confined to very few forms, and those the oldest. Therefore, as well as on anatomical grounds, we infer that the prevalence of these characters denotes a primitive order.

There is considerable parallelism of development between early Inadunate forms of Dicyclica and Monocyclica; nevertheless, most of the Monocyclic genera fall into clearly marked groups, with which no Dicyclica can be confused. The Hybocrinidae and *Stephanocrinus* are here taken first, because of their simple structure and resemblance to Eublastoidea. At a very early period the Heterocrinid type must have arisen, through horizontal bisection of RR (*antea*, p. 112) and branching of arms. *Iocrinus* and *Anomalocrinus* may be early offshoots from that line of descent; *Herpetocrinus* and the Calceocrinidae are other remarkably specialised offshoots, the latter surviving to Carboniferous times. Starting afresh from the Hybocrinidae, the exaggeration of size in certain RR became more pronounced in the Pisocrinidae, which, by addition of supplementary radials and arms, lead up through *Calycanthocrinus* and *Mycocrinus* to *Catillocrinus*, a type presenting a strange convergence to *Halysiocrinus*. *Zophocrinus*, *Allagecrinus*, and certainly *Haplocrinus* appear to be aberrant from this line of descent. The more regular Symbathocrinidae, with their simple arms, represent either the direct descendants of the Hybocrinidae or a return from the Pisocrinidae to a more normal structure.

The Carboniferous *Belemnocrinus* simulates many Dicyclica in the complexity of its anal tube, but in arm-structure may be regarded as intermediate between the Heterocrinidae and certain Neozoic Monocyclica. Of these latter, the first to appear are the Plicatocrinidae, and from them spring the Jurassic *Saccocoma* and the Recent *Hyocrinus.*

FAMILY 1. HYBOCRINIDAE. Monocyclica Inadunata, in which RR differ but slightly in size and shape, except r. post. R, which supports on its left shoulder the proximal plate (*x*) of the rudimentary anal tube, when present, while its right shoulder is separated by a slanting suture from the lower part of the plate and bears an arm. BB, 5. Arms, 3-5, unbranched, uniserial, non-pinnulate, less wide than RR. O, so far as known, large, with traces of hydrospires, not separated from RR by supplementary plates ; post. O cut into by anus and pierced by hydropore. Amb rest on adjacent edges of O. Genera—*Hybocystis*, Wetherby (1880, see p. 95, Fig. I.) ; *Hybocrinus*, Billings (1857,-59 ; syn. *Indianocrinus*, Mill. & Gurl.), Ordovician and Silurian, N. America (Figs. LVII. 3, VI. and XXXVI.) ; *Hoplocrinus*, Grewingk (1867), Ordovician, Russia, includes *Baerocrinus* (Fig. LVII. 1, 2, 4). For chief literature see W. & Sp. (91).

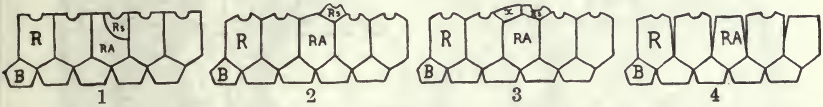


FIG. LVII.

Hybocrinidae. 1, *Hoplocrinus dipentas* (type); 2, *Hoplocrinus dipentas* (var.); 3, *Hybocrinus tumidus ;* 4, "*Baerocrinus*" *Ungerni.*

FAMILY 2. STEPHANOCRINIDAE. Monocyclica Inadunata, with 5 equal RR, each bearing an arm in a deep radial sinus. BB, 3, the unfused B being usually r. ant. as in Blastoidea. Arms branched. O large, with traces of hydrospires (?) at their junction with RR ; anus at junction of post. O with RR, with minute valvular covering. Amb, often fused, rest on adjacent edges of O, and 5 large ones, often fused, cover the peristome. Genus—*Stephanocrinus*, Conrad (1842, see p. 96, Fig. II.), Silurian, N. America and Britain, and as "*Rhombifera mira*" in Bohemia. The arms are said to branch, but no two observers agree as to the mode of branching, and in fact it seems to differ in the various ambulacra of the few specimens that preserve the arms (R. P. Whitfield *in litt.*).

FAMILY 3. HETEROCRINIDAE. Monocyclica Inadunata, with *x* usually resting on left shoulder of r. post. Rs, and partly on right shoulder of l. post. R, but sometimes sunk between the two, and always supporting a long anal tube. BB, 5. Arms, 5, with proximal Br usually full width of RR ; isotomous or heterotomous, or bifurcate with armlets ; non-pinnulate. 5 O, without perisomic plates, have been observed in *Heterocrinus heterodactylus juvenis*, but the relations of Amb to tegmen are unknown. Genera—*Iocrinus*, Hall (1866), Ordovician, N. America (Figs. XXVI. 1 ; XXVIII. ; and LVIII. 1); primitive in its isotomous arms, and RR similar in shape and undivided, except r. post. R, from which an upper portion, in shape like an axillare, is separated by a horizontal suture, and bears an arm on its r. shoulder, and on its l. shoulder a line of ossicles supporting an anal tube. Therefore for this line of descent, such a position of the median dorsal rib of the anal tube is considered primitive (among Dicyclica a similar stage is presented by *Merocrinus*). Anal tube somewhat complicated. Stem markedly pentagonal, with 5 interradial sutures. *Heterocrinus*, Hall (1843, em. S. A. Miller, 1889, syn. *Stenocrinus*, W. & Sp.); *Ectenocrinus*, Miller (1889); and *Ohiocrinus*, W. & Sp. (1886), are best known from Ordovician, N. America, but certainly had representatives in Europe, where also they were preceded in Cambrian seas by "*Dendrocrinus cambriensis*," Hicks (1873), which seems allied to *Iocrinus*. They agree in the transverse bisection of r. and l. ant. RR, in addition to r. post. R (exceptionally l. ant. R is simple, and ant. R may be compound in its stead); in the partial entry of the proximal plate of the anal tube into the cup, since it now rests partly on l. post. R, though more intimately connected with r. post. R*s* (Fig. XXVII.); in the departure from isotomy in the direction of two rami with armlets. In *Heterocrinus*, *Ohiocrinus*, and *Iocrinus* the stem is pentagonal and quinquepartite; in *Ectenocrinus* almost circular and tripartite. The anal tube is straight and narrow in *Heterocrinus* and *Ectenocrinus*, spirally coiled in *Ohiocrinus* (cf. *Botryocrinus*, *Streptocrinus*). *Ectenocrinus* has almost reached a pinnulate stage of arm-branching, since the Br form syzygial pairs. *Anomalocrinus*, Meek & Worthen (1885; syn. *Ataxocrinus*, Lyon), Ordovician, N. America, differs from the last three genera: (1) in greater irregularity of RR, l. post. R being larger than the others and often bisected vertically (l. ant. R or ant. R, as well as r. post. R, are horizontally bisected as usual); (2) in its peculiar arm-branching (Fig. LVIII. 4). *Herpetocrinus*, Salter (1873; synn. *Ophiocrinus*, Charlesworth; *Myelodactylus*, Ang. and [?] Hall; [?] *Brachiocrinus*, Hall. Fully described, Bather, 1893), Silurian, Europe, and probably N. America. Crown bent, in the transversal plane, back on the stem, which is then coiled around it in the opposite direction (Fig. LIX.). The coil could be tight, or could be uncoiled and the crown exposed; the movement was effected by an elastic ligament towards the inner margin of the columnals, counteracted by strong muscles towards the outer margin, the fulcrum being a transverse ridge. Columnals show

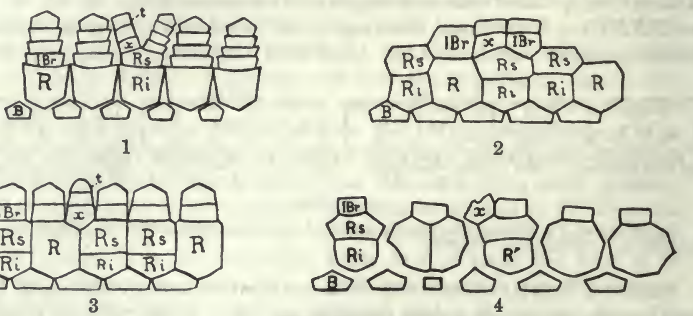


FIG. LVIII.

Heterocrinidae. 1, *Iocrinus;* 2, *Heterocrinus bellevillensis;* 3, *Ectenocrinus;* 4, *Anomalocrinus.*

traces of original pentamerism, but over the greater part of the stem are crescentic in section, the concavity being on the inner margin. Cirri, borne on the horns of the crescent, vary in their arrangement in different species. No root in adult. One ray missing; other RR all compound, except l. post. R sometimes; x lower than in other Heterocrinidae, partly rests on r. post. R*i* (the radianal, RA). The tube outwardly resembles a series of Br and covering-plates. Arms slightly heterotomous. The remarkable resemblance of the coiled cirriferous stem to a pinnulate, canaliculate arm has misled most writers; for the crown is rarely visible (*vide* p. 134). Family 4. Calceocrinidae. Monocyclica Inadunata, with the essential characters of typical Heterocrinidae, the l. ant., r. ant., and r. post. RR being compound, and the arms branching primitively on the plan of *Heterocrinus heterodactylus;* but with the following modifications induced by the bending down of the crown:—the r. post. IR lies alongside the stem; the l. ant. R lies away from the stem; the plane thus marked is one of a gradually increasing bilateral symmetry; r. post. arm always

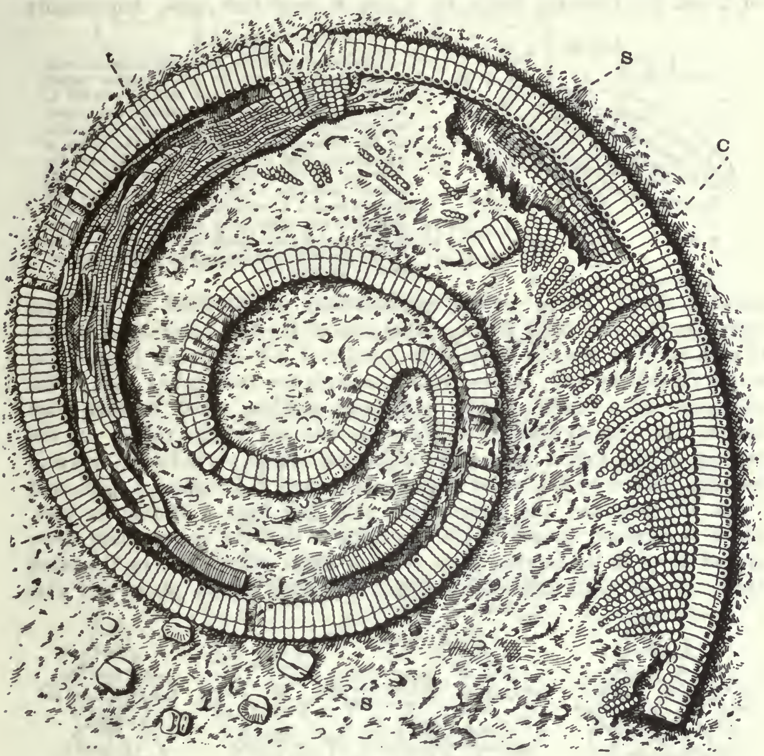


Fig. LIX.

Herpetocrinus Fletcheri, in its natural coiled position, the cirri which covered the crown having been removed. *C*, cirri; *S*, longitudinal suture of stem; *t*, anal tube. (After Bather, 1893.) × $\frac{3}{2}$.

absent, its place being occupied by anal tube; the tube encroaches on r. ant. arm, so that this too disappears; r. post. Rs and r. ant. Rs fuse to form a T-shaped piece supporting anal tube; the T-piece atrophies, and the tube then rests on the corresponding inferradials; the simple RR (l. post. and ant.) increase in size, forming the sides of the cup and bending round on the adcolumnal side where the anal tube is, as well as on the acolumnal side, where they eventually meet between the two halves of l. ant. R; the arm borne by l. ant. R may fork once, but usually remains simple, owing to the extraordinary development of the arms borne by the two large RR on either side of it; the adcolumnal ramus of each of those arms is reduced to a series of 3-8 axillaries (main-axils) which lie side by side, curving round towards the anal tube; each main-axil gives off a branch which itself bears armlets, which in turn may assume the regular nature of pinnules, and are rarely visible on the exterior of the folded arms; the acolumnal ramus dwindles in size and becomes hidden by the other branches; r. post. B atrophies, l. post. and l. ant. BB fuse, and the three plates thus left form a triangular base, which is regularly hinged to the l. ant. R*i*, so that the crown could move up and down in the sagittal plane of its bilateral symmetry; on the other hand, the columnals have each a slight curvature in this plane, and this kept the stem itself rigid. The various stages in the evolution are marked by 4 genera (Fig. LXI.): *Castocrinus*, Ringueb. (1889), Ordovician, N. America; *Euchirocrinus*, Meek & Worth. (1873; synn. *Cheirocrinus*, Hall *non* Eichw.; *Cremacrinus*, Ulr.; *Proclivocrinus*, Ringueb.), Ordovician and Silurian, N. America; *Calceocrinus*, Hall (1852, em. Ringueb., 1889; synn. *Cheirocrinus*, Salter, *nom. nud.*; *Pendulocrinus*, Austin, MS.; ? *Deltacrinus*, Ulr.), Silurian and Devonian, N America and Europe; *Halysiocrinus*, Ulrich (1886, em. Bather, 1893), Carboniferous, N. America. For history and morphology see Bather (1893).

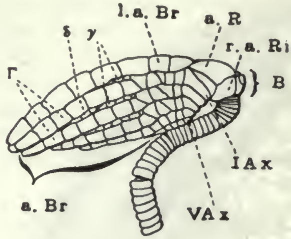


FIG. LX.

Calceocrinus tucanus, from the anterior side. *B*, the base, hinged to left anterior radial, which is out of sight, and flexibly jointed to *r.a.Ri*, right anterior inferradial; the superradials of this and of the corresponding radial on the other side are hidden by the series of main-axils, *IAx* to *VAx*, which support the branches of the two large side-arms; the visible side-arm, *a.Br*, is the anterior, and springs from *a.R*, anterior radial; its diminished branches are seen at γ and δ, its enlarged branches at Γ; the single arm along the upper side is the left anterior (*l.a.Br*). (After Bather, 1893.) Natural size.

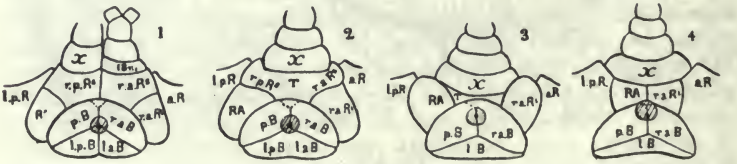
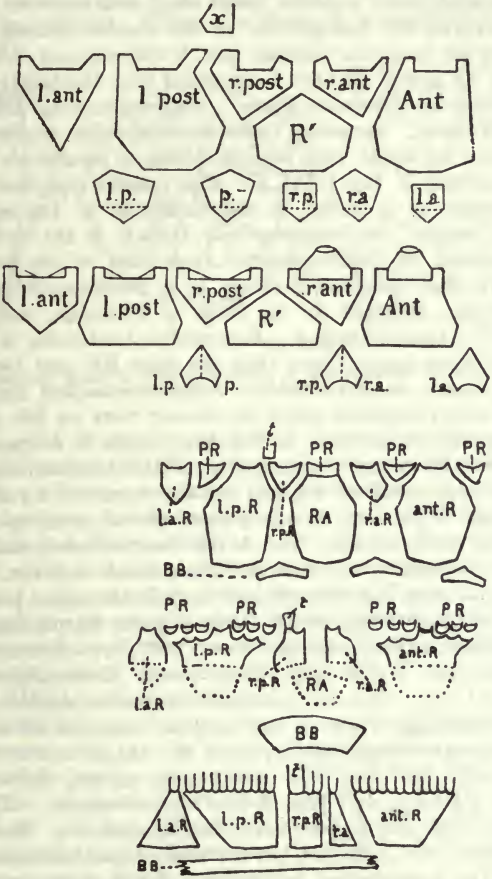


FIG. LXI.

Diagrams illustrating the structure of the posterior area in 1, *Castocrinus*; 2, *Euchirocrinus*; 3, *Calceocrinus*; 4, *Halysiocrinus*.

Family 5. Pisocrinidae. Monocyclica Inadunata with l. post. R and ant. R much larger than the other RR; r. post. R is the only compound R transversely bisected, and its lower half separates r. post. R*s*, and r. ant. R from BB, and forms with the two large RR the greater part of the dorsal cup. Arms unbranched and non-pinnulate. An anal tube usually present, resting on post. RR or on their processes. Genera—*Pisocrinus*, de Koninck (1858), Silurian, N.-W. Europe and N. America (Fig. LXII. 1; see also XVIII. 5), and *Triacrinus*, Münster (1839, syn. *Trichocrinus*, J. Müller, 1856), Devonian, Germany (Fig. LXII. 2), differ in that the former has 5 BB, the latter 3. But incipient fusion of BB is seen in *P. ollula*, and 5 BB occur in some *Triacrinus*. The anal tube closely


x
l.ant
l post
r.post
r.ant
Ant
R′
l.p.
p.
r.p.
r.a
l.a
l.ant
l.post
r.post
r.ant
R′
Ant
l.p
p.
r.p.
r.a.
l.a.
t
PR
PR
PR
PR
l.a.R
l.p.R
r.p.R
RA
r.a.R
ant.R
BB
PR
PR
t
PR
PR
l.p.R
ant.R
r.p.R
RA
r.a.R
l.a.R
BB
t
l.a.R
l.p.R
r.p.R
r.a
ant.R
BB

1. *Pisocrinus.*

2. *Triacrinus.*

3. *Calycanthocrinus.*

4. *Mycocrinus.*

5. *Catillocrinus.*

Fig. LXII.

Pisocrinidae and Catillocrinidae. *PR*, pararadials; *t*, anal tube plate = *x*; *R′*, radianal = *RA*; other letters as usual. In *Mycocrinus* the radianal and lower parts of RR are hidden and therefore represented by dotted lines.

resembles an arm, and its presence was first notified in 1893. The relations of the cup-plates, till then misunderstood, were thus shown to be essentially the same as in the majority of Monocyclica, while the origin of *Calycanthocrinus*, *Mycocrinus*, and *Catillocrinus* became clear. This was confirmed by Jaekel (1895). *Pisocrinus* was shown by Wachsmuth to have 5 O surrounding a peristomial space; a groove passed along each interoral suture, and probably conveyed the food-grooves to the central opening. The rectum passed into the anal tube between post. O and adjacent RR. An anal tube is said by Jaekel to have been absent from the thinly plated species of *Triacrinus* in Devonian slates. *Calycanthocrinus*, Follmann (1887), Lower Devonian, Germany, shows a remarkable modification, in the introduction of small arm-bearing plates ("pararadials" PR), in the positions shown in Fig. LXII. 3. This may be compared with the vertical bisection of a radial in *Anomalocrinus* or the addition of 5 "interradial radials" in *Promachocrinus;* but it is the first stage of a process continued in Catillocrinidae. It is hard to see how this process could have been inaugurated except as a discontinuous meristic variation (cf. Bateson, *Materials for the Study of Variation*, chap. xvii. 1894). FAMILY 6. CATILLOCRINIDAE. Monocyclica Inadunata, in which l. post. R and ant. R are much larger than the other RR, and bear PR, usually fused to them; no RA visible. Arms unbranched and non-pinnulate. Anal tube resembling arms, but stouter, rests on left process of r. post. R. Genera—*Mycocrinus*, L. Schultze (1866, W. & Sp., 1886; Jaekel, 1895), Middle Devonian, Germany (Fig. LXII. 4), differs from *Calycanthocrinus* in the suppression of RA and the PR borne by it; the still greater size of l. post. R and ant. R, which now bear 6-7 arms apiece, *i.e.* 15-17 arms to the whole crown. The 3 BB become fused, while the 10-12 PR are usually fused with the large RR on which they rest. The increase in size of the large RR takes place chiefly in the upper part; all the RR rest on the basal circlet, which forms a knob sharply separated from them. *Catillocrinus*, Shumard ex Troost (1860, syn. *Nematocrinus*, Meek & Worthen; see W. & Sp., 1886), Lower Carboniferous, N. America (Fig. LXII. 5). The cup has here resumed a shallow basin-shape, and differs from *Mycocrinus* in the complete fusion of BB and the still greater lateral extension of the l. post. R and ant. R in their upper regions. Those large RR now bear 15-31 arms apiece, there being usually more on ant. R than on l. post. R (cf. *Calycanthocrinus*). The PR are absolutely fused with RR, or were never developed at all. The basal circlet projects upward on l. ant. side, but is almost hidden by the stem on the other side. The arrangement and shapes of the plates curiously resemble those which obtain in *Halysiocrinus*, while the arms may be compared to the branches that spring from the main-axils in that genus. A similar result has been attained by two lines of development, which, in their initial stages, were as different from one another and from the normal type as could well be. The relationship of these forms is a problem that would repay yet deeper study. FAMILY 7. ZOPHOCRINIDAE. Monocyclica Inadunata, with 3 BB, 2 equal and 1 larger; 4 RR, 1 rather larger than the rest, and probably equals r. and l. post. fused; 5 O form solid tegmen, post. O being the largest, and r. and l. ant. O the smallest and, what is rather unusual, not meeting post. O in centre; anus unknown; 5 groups of short arms lie where the interoral sutures meet the RR, which is not in the middle of any RR except ant. R (see Fig. LXIII. 2); each arm-group appears to consist normally of 3 elements, 2 inner and 1 outer, all springing equally from the calyx; stem with small axial canal. Genus—*Zophocrinus*, S. A. Miller (1891), Silurian, Indiana (Fig. LXIII.). Theca pear-shaped; Miller says there are 5 arm-plates in each group, and this may be so in some specimens; these arm-plates may be compared with the arms of Catillocrinidae, but whether they bore further Br is uncertain. The tetramerism of this genus affects the cup only, and was produced by fusion, not by atrophy as was probably the case in *Herpetocrinus.*

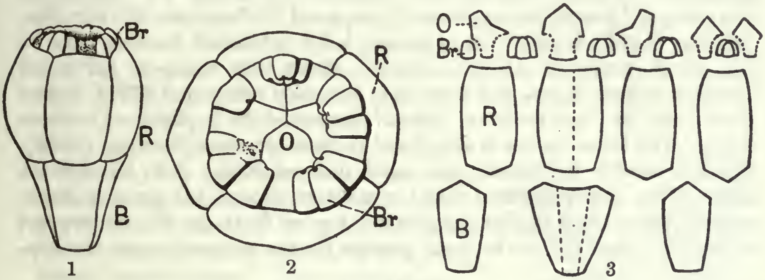


Fig. LXIII.

Zophocrinus howardi, from a specimen in the collection of Hon. F. Springer. 1, from posterior, × $\frac{4}{1}$; 2, oral surface, × $\frac{10}{1}$; 3, dissection of plates.

Family 8. Haplocrinidae. Monocyclica Inadunata, with 5 BB, 5 RR, of which l. ant., r. post., and r. ant. are compound; tegmen composed solely of 5 O, one being pierced by a pore (? anus + hydropore); 5 arms, unbranched and non-pinnulate, the food-grooves supposed to be subtegminal. Genus—*Haplocrinus*, Steininger (1837; *Aplocrinus*, d'Orb.; see W. & Sp., 1886), Devonian, Europe and N. America (Figs. XXXV. and LXIV.); resembles the typical Heterocrinidae in its cup, the Pisocrinidae in its arms, and *Allagecrinus* in its tegmen. The pore in post. O was discussed on p. 126. Family 9. Allagecrinidae. Monocyclica Inadunata, with 5 BB, 5 RR all simple, but of unequal and variable size, the larger ones often bearing 2 arms, while some arms may occasionally be absent or diminished in size; tegmen composed in the young of 5 O, one pierced by a pore (? anus + hydropore); 5 arms unbranched and non-pinnulate, the food-grooves supposed to be subtegminal. Genus—*Allagecrinus*, Etheridge & Carpenter (1881, restricted by W. & Sp., 1886), Lower Carboniferous, N. America, Upper Carboniferous, Scotland, resembles *Haplocrinus* in its tegmen, while the duplication of arms is

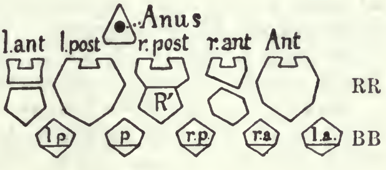


Fig. LXIV.

Dissection of cup of *Haplocrinus*. *R'* = radianal.

reminiscent of *Calycanthocrinus;* here, however, the RR are axillary, and PR not developed. Rowley (1895) has described calyces less than ·5 mm. high. FAMILY 10. SYMBATHOCRINIDAE. Monocyclica Inadunata, with 5 simple RR, bearing 5 unbranched, non-pinnulate arms, which rest as a rule on broad articular facets projecting adorally in "muscle-plates," corresponding to the muscle-fossae. Genera—*Phimocrinus* (Low. and Mid. Devonian, Europe), *Stylocrinus* and *Stortingocrinus* (Mid. Devonian, Europe), *Symbathocrinus*, including *Lageniocrinus*, which is probably its young (Upper Devonian and Lower Carboniferous, Europe and N. America). *Phimocrinus*, Schultze (1866), is primitive in having 5 BB, while all the rest have 3; the oldest species, *P. Jouberti*, Oehlert, shows clear traces of horizontal suture in r. post., r. ant., and l. ant. RR, the usual compound RR of typical Heterocrinidae; the proximal plate of the anal tube is placed as in those forms. The latter feature is also found in *Stortingocrinus*, Schultze (1866), which is notable for having the small unfused B in l. post. IR, and the angles of the columnar canal radial in position, though the genus is Monocyclic. *Stylocrinus*, Sandberger (1850), has no facet on RR for support of an anal tube, nor is the usual passage for the rectum seen in the cup-wall; therefore one cannot orient the small B; the anus probably pierced post. O. *Symbathocrinus*, Phillips (1836), has small B in l. ant. IR, as in Platycrinidae; the anal tube rests on the shoulder of r. post. R; 5 O, all small, post. O being the largest and separated from the muscle-plates of the adjacent RR by the passage of the rectum (Fig. LXV.). The family is not clearly defined, and its Middle Devonian members present remarkable, though superficial, resemblances to the contemporary Cupressocrinidae.

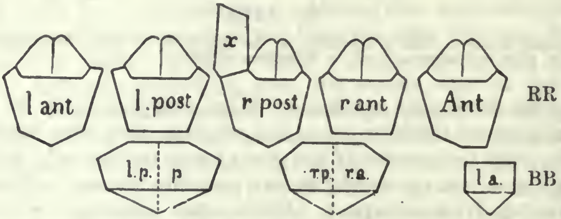


FIG. LXV.

Dissection of cup of *Symbathocrinus*. The projections on the *RR* are muscle-plates.

FAMILY 11. BELEMNOCRINIDAE. Monocyclica Inadunata, with 5 BB, 5 simple RR, each supporting by a slightly excavate facet an arm which forks on $IBr_{4 \text{ or } 5}$; each ramus, with numerous syzygies in the proximal portion, bearing ramuli on alternate sides of most epizygals and of all ordinary distal brachials; single narrow anal in radial circlet, resting on post. B, and supporting a large anal tube composed of alternating hexagonal plates, folded on their lateral margins. Genus—*Belemnocrinus*, White (1862), Lower Carboniferous, N. America. Dorsal cup elongate, its plates solid, and thecal cavity a narrow canal below and shallow excavation above, thus resembling that of many Neozoic crinoids. *B. typus* has no cirri on the stem, which is circular in section; *B. florifer* has a stellate stem of true Monocyclic type, with 3 or 4 cirri to each node.

Missouricrinus, S. A. Miller (1891), Burlington group, if truly Monocyclic, must be placed near here.

FAMILY 12. PLICATOCRINIDAE. Monocyclica Inadunata, with BB fused into a knob-like support; 4 or 6 (exceptionally 3, 5, 7, or 8) simple RR, enclosing wide thecal cavity, each supporting an arm, which forks on IBr_1; IIBr wedge-shaped, united by perforate articulation, not, so far as known, by syzygy, regularly pinnulate; pinnulars tend to fuse. Tegmen unknown. Columnals cylindrical, with radiately striated joint-surface. For full account, and for the evidence of the axial canals passing from RR into the fused basal circlet, so proving that it is no columnal, see Jaekel (1893). Genera—*Plicatocrinus*, Münster (1839), Upper Jura, Germany (Fig. LXVI.), thin RR enclose a wide and deep thecal cavity, facets from $\frac{1}{2}$ to $\frac{4}{5}$ width of R, crescentic, without large muscle-plates; proximal pinnules composed of 3 pinnulars, which in succeeding pinnules are fused to a solid piece. *Tetracrinus*, Münster (1839), Upper Jura, France and Germany, has thick RR with strong muscle-fossae. The occasional occurrence of 3, 5, 7, or 8 rays shows that the normal 4 and 6 arose from the more usual 5 as sports (*i.e.* discontinuous meristic variations). FAMILY 13. HYOCRINIDAE. Monocyclica Inadunata, with 3 thin BB, the smaller one in l. post. IR; 5 RR, thin, broad, and spade-shaped, with a slight axial fold running straight up the middle from the subjacent B and ending in a narrow facet; 5 arms, bearing unbranched alternating ramuli, which may be modified in their proximal portions for reception of ripe gonads; Br long, cylindrical, with deep, narrow ventral groove; below the first ramule, which is on the right of each arm, are 6 Br, with the joint between each pair a syzygy; between successive ramuli are 3 Br, united by syzygies; proximal ramuli the longest, and the following ones proportionately shorter, so that they all terminate on the same level as the arm ends; 5 triangular O, separated from RR by iAmb and Amb, cover the wide mouth and circumoral tentacles; each O as a rule pierced by a water-pore, and post. O by 2; water-pores also pierce several iAmb, but not in post. IR; anal tube reduced to a small cone towards the left of the post. interambulacrum; columnals cylindrical, slightly higher than wide, united by discs of ligament-fibres, joint-surfaces hollowed and plain or indistinctly striate, with stellate axial canal; no cirri; root unknown. The sole living representative of the order is the unique species *Hyocrinus bethellianus*, W.-Thomson (1876, Fig. LXVII.), dredged by H.M.S. *Challenger* 30 miles W. of Crozet Is., in the Southern Ocean, while columnals are said to have been found in Mid-Atlantic just N. of the Equator; see P. H. Carpenter (1884).

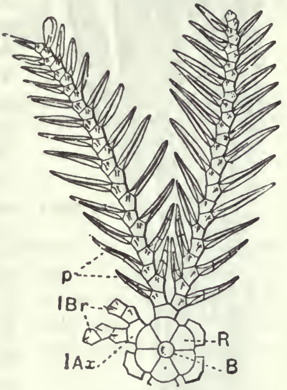


FIG. LXVI.

Plicatocrinus Fraasi, from aboral surface with one outstretched arm complete. (Adapted from Zittel, 1882, × $\frac{3}{2}$.)

Evidence for its truly Monocyclic nature is wanting; but in the absence of proof to the contrary, it must be left in this, apparently natural, position. The stem is not unlike that of some Plicatocrinidae; the branching and syzygies of the unforked arms remind one of the structure in the arm-rami of *Belemnocrinus* and *Saccocoma;* the cup is not unlike that of *Plicatocrinus Fraasi.* The only specimen at all complete is a male, with testes probably mature and swelling out in the proximal portions of the proximal ramuli; in these regions each ramular supports 2 or 3 square side-plates on either side, and these support the covering-plates. The orals could probably open to expose the funnel-shaped gullet, which leads into a narrow gut with single dextral coil; glandular ridges line the gullet and first part of the gut. The intra-thecal connective tissue contains no spicules. FAMILY 14. SACCOCOMIDAE. Monocyclica Inadunata, in which 5 RR and a minute centrale enclose a large spheroidal thecal cavity; each R has a prominent median ridge ending in a narrow facet, which supports a thin arm, forking on IBr_2; beginning at about $IIBr_{15}$, each ramus gives off from every 3rd Br unbranched alternating ramuli arranged as in *Hyocrinus;* the rami and ramuli are usually found rolled up in their distal portions; Br cylindrical, elongate; Iax and the more proximal IIBr may bear lateral, paired, wing-like expansions, which in the more distal Br and the ramulars are always represented by delicate trellised processes, with thicker upper and under margins, which it is conjectured supported a continuous membrane; no stem; all skeletal elements very thin and coarsely reticulate. Genus—*Saccocoma,* L. Agassiz (1834; syn. *Euryale,* König), Solenhofen Lithographic Stone, Upper Jura (Fig. LXVIII.). Jaekel, who has admirably elucidated the structure and affinities of this wonderfully specialised crinoid (1893), considers that the arms were swimming-organs, the food-groove, ambulacral, and genital systems being atrophied at their distal ends, and that the animal was pelagic, floating in enormous swarms in the peaceful lagoons of Eichstädt and Solenhofen.

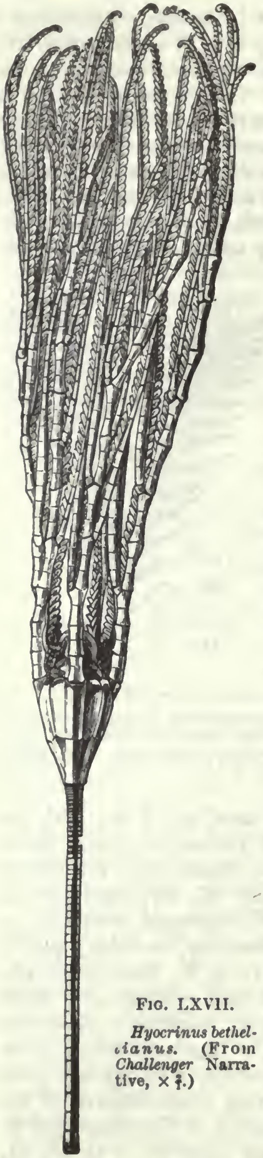


FIG. LXVII.

Hyocrinus bethellianus. (From *Challenger* Narrative, × $\frac{2}{1}$.)

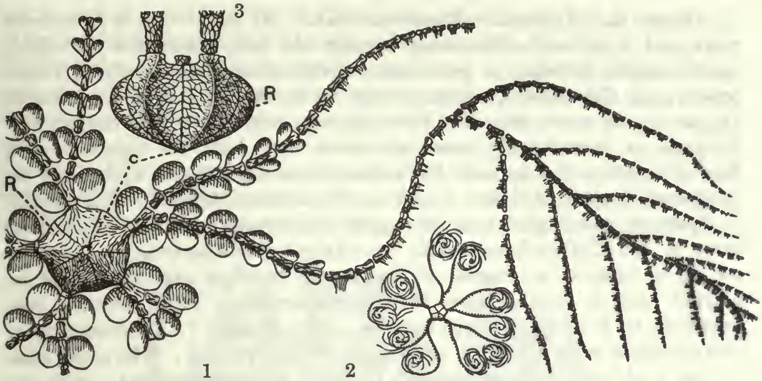


FIG. LXVIII.

Saccocoma. 1, *S. tenella*, from aboral surface (after Jaekel, $\times \frac{1}{1}$). 2, *S. pectinata*, from aboral surface, to show coiling of arm-branches ($\times \frac{1}{2}$). 3, *S. pectinata*, cup and proximal brachials from side (after Zittel, $\times \frac{5}{2}$).

ORDER 2. **Adunata** (Bather, 1899).

Monocyclica with dorsal cup primitively confined to the patina and an occasional single anal; tegmen solid; portions of the proximal Br and their Amb tend to be rigidly incorporated in the theca. Arms fork once to thrice, and bear pinnules on each or on every other Br. BB fused to 3, 2, or 1. (*Eucladocrinus* and Acrocrinidae offer peculiar exceptions to this diagnosis.)

The genera of this order have been referred, in whole or part, to the Camerata or their equivalents by most recent writers. But most of the Silurian genera here included are admitted as close allies of Monocyclica Inadunata. If so, then they were derived from Inadunata ages after the typical Camerata had appeared. Moreover, though the Devonian and Carboniferous descendants of these Silurian genera became modified after the fashion of the Camerata, there is scarcely one in which the modification is so great as in the simplest Camerate. The order is divisible into two groups—*A.* with RR in contact all round the cup, and base consequently pentagonal in outline; *B.* with RR separated by an anal plate in post. IR, and base consequently hexagonal in outline. The relations of these groups are not clear. *B.* may be derived from *A.* by sudden intercalation of an anal, or *A.* and *B.* may have descended independently from Inadunata; the absence of *B.* from Silurian rocks renders the former hypothesis more probable. There is no difficulty in imagining the descent of early genera of *A.*, such as *Cordylocrinus* and *Coccocrinus*, from Hybocrinidae in which the cup had become as symmetrical as in, say, *Stephanocrinus* while the arms had passed through regular dichotomy to a stage with ramuli, as in *Ectenocrinus*. The actual intermediate form is not yet known, but that it will be found among Ordovician crinoids is a legitimate inference.

Group A. Family 1. Platycrinidae. No anal. BB 3 (= 2 fused pairs and 1 unfused, this being usually the left, sometimes the right, antero-lateral) forming a pentagon. *Cordylocrinus*, *Hapalocrinus*, *Coccocrinus*, and *Cylicocrinus*, which appear in the Silurian and continue to Devonian, are more primitive than the rest. *Marsipocrinus*, though also Silurian, is considerably more advanced, and may be regarded as a first attempt at the typical *Platycrinus* structure; it was apparently an unsuccessful attempt, since it left no descendants, although Wachsmuth & Springer and Jaekel seem to regard *Platycrinus* as such. *Platycrinus* came in the Carboniferous, with its offshoot *Eucladocrinus*, and, unless we are to imagine a reversal of the general trend of evolution, must be derived from a simpler form than *Marsipocrinus*. These facts are best presented by instituting 3 sub-families. Sub-Family 1. Coccocrininae. Platycrinidae with IBr 2 (3 in *Hapalocrinus Victoriae*); IIBr more than 2; few Amb and iAmb in tegmen; (?) anal tube rarely present; stem circular in section; lumen small and round. Genera—*Coccocrinus*, J. Müller (1855, syn. *Amblacrinus*, d'Orbigny *pars*, 1849), Silurian of America, Devonian of Europe; O large, symmetrical, almost covering the tegminal ambulacra; iAmb 1 or 3; anus between O and iAmb; arms apparently delicate, fork once, distal portions unknown. *Cylicocrinus*, J. Müller (1855, as *Culicocrinus;* Jaekel, 1895), Devonian, Germany (Fig. XL.), differs from *Coccocrinus* chiefly in having heavy biserial arms. *Hapalocrinus*, Jaekel (1895, em. Bather, 1897; includes *Agriocrinus*, *Thallocrinus*, and *Clematocrinus*, Jaekel), Silurian of England, Australia, and (?) N. America, Devonian of Germany (Fig. LXIX.); O small; iAmb more than 1; Amb visible between O and iAmb; arms fork once, sometimes twice, varying in this respect in the same species, or even individual; IIBr (and IIIBr when present) uniserial, or slightly in zigzag, bearing alternately disposed pinnules, either on each or on every other Br; cirri at the root, and often on nodals. *Cordylocrinus*, Angelin (1878; W. & Sp., 1897; Bather, 1897), Silurian of Gotland and England, Lower Devonian of N. America; differs from *Hapalocrinus* in having compound IIBr, each of which bears a pinnule on each side. Sub-Family 2. Marsipocrininae. Platycrinidae with one IBr; IIBr, if not finials, one or two; many Amb and iAmb in tegmen; no anal tube; stem circular in section; lumen large and quinquelobate. Genus—*Marsipocrinus*, Bather (1889, nom. nov. pro *Marsupiocrinus*, Phillips, 1839, *non* de Blainville, 1830; syn. *Cypellocrinus* vel *Cupellaecrinus*, Shumard, 1866, ex Troost MS., *non* Steininger), Silurian, N.-W. Europe and N. America; arrangement of cup-plates shown in Fig.

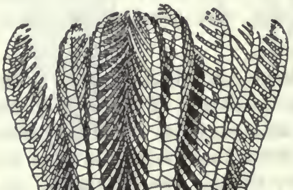


Fig. LXIX.

Hapalocrinus retiarius, from Brit. Mus. E5615. *c*, cirri; *iBr*, interbrachials. The suborals of Jaekel. Other letters as usual. × 3.

LXX., and of tegmen in Fig. XXXII. ; O rather small, pushed anteriorly, and asymmetrical; tegminal IAmb and IIAmb distinctly visible ; arms fork once or twice, stout, biserial, with large pinnules ; no cirri on column. The large size of the cup is accompanied by development of stroma-strands across the sutures. The large tegmen permitted a Gastropod (*Platyceras*) to attach itself above the anus and live on the excrement ; this is seen in many of the larger Adunata and Camerata and a few other crinoids (Keyes, 1888). SUB-FAMILY 3. PLATYCRININAE. Platycrinidae with IBr 1 (rarely 2), IIBr 2 (rarely 3) ; tegminal Amb and iAmb usually more than in Coccocrininae, fewer than in Marsipocrininae ; anal tube often present ; section of stem circular near the cup, elliptic or rhomboid below, with fulcral ridge following long diameter ; lumen small and round. Genera—*Platycrinus*, Miller (1821, W. & Sp., 1897 ; synn. *Centrocrinus* and *Pleurocrinus*, Austin ; *Edwardsocrinus*, d'Orb.), Devonian (1 species), Carboniferous, Europe and N. America (Fig. LXXI.) ; 1-3 iAmb always rest on the adjacent shoulders of the RR in each IR, and consolidate a varying number of Br and Amb with the calyx ; arms fork once to thrice (exceptionally more), the dichotomy often irregular, producing 6 rami to the arm ; columnals have a slight skew, so that the fulcral ridge of the proximal surface lies at an angle to that of the distal surface ; thus the flattened stem, which otherwise could

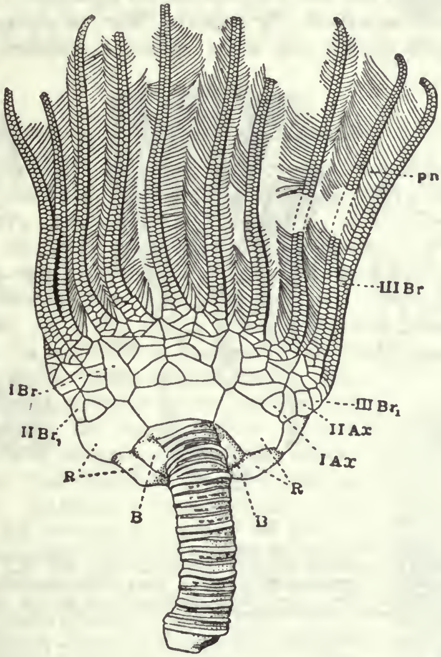


FIG. LXX.

Marsipocrinus, from Brit. Mus. E6519. *pn*, pinnules ; other letters as usual. Nat. size.

move only in one plane, has a spiral twist that enables it to bend in any direction (Fig. XLIX. 5, 6). *Eucladocrinus*, Meek (1871, W. & Sp., 1897), Carboniferous, N. America; appears late in the history of *Platycrinus*, from which it was evolved polygenetically by modification of the arms; two main rami to each arm (sometimes only one ramus) composed of biserial Br, with large almost rigid Amb, form tubular extensions of the thecal cavity, and give off on alternate sides short, biserial ramuli, which in turn bear pinnules (Fig. LXXI. 4). This sketch of the evolution of the Platycrinidae is confirmed by the ontogeny of *Platycrinus*. In young stages (Fig. LXXI. 2) the basal cup is relatively shallower; RR less high; columnals circular in section; Br uniserial, later on zigzag, and longer; pinnules relatively stouter and wider apart; O relatively larger, and occupying greater part of tegmen. From this obviously Coccocrinine stage, the change to the mature *Platycrinus* has been observed in many species.

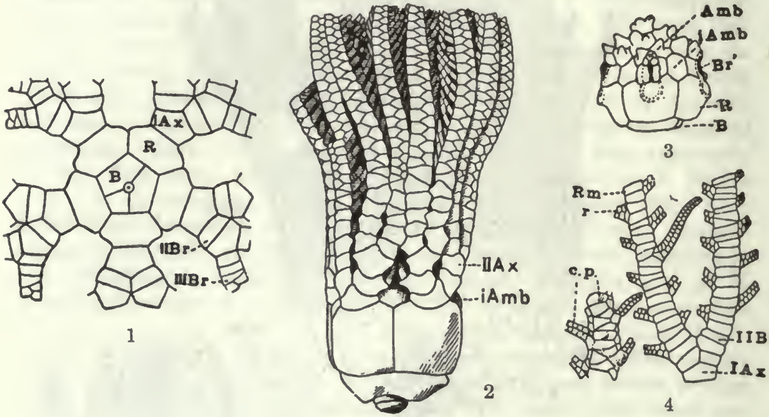


Fig. LXXI.

Platycrininae. 1, aboral view of cup and proximal brachials of *Platycrinus subspinosus* (after Wachsmuth & Springer). 2, crown of young *P. Huntsvillae*, from Brit. Mus. E6778. × ⅘. 3, calyx of *P. eminulus*, anterior view (after W. & Sp.). 4, arms of *Eucladocrinus millebrachiatus*, oral surface showing covering-plates (*c.p*) and aboral surface (after W. & Sp.). *Br'*, articular facet for arms; *Rm*, ramus; *r*, ramule; other letters as usual. All (exc. 2) two-thirds natural size.

Group B. Family 2. Hexacrinidae. Cup formed of 1, 2, or 3 BB, forming a hexagon; 5 RR; and 1 anal in line with RR. The family is closely related to the Platycrinidae, but differs in the hexamerous symmetry; also, as a consequence of this, in the presence of an interbasal suture in post. IR, whereas in Platycrinidae the nearest to that position is in r. post. radius. Genera—*Hexacrinus*, Austin (1843, Schultze, 1867, W. & Sp., 1897), Devonian, Europe and N. America (Fig. LXXII.); BB 3; IBr, 2 united by syzygy in America, only 1 in Europe; arms with 2 rami, bearing ramuli on one or both sides at intervals; Br uniserial, and all except axillaries bear pinnules; tegmen as in *Platycrinus*; stem circular in section, with small round lumen. *Arthracantha*, Williams (1883, syn. *Hystricrinus*, Hinde, 1885), has theca of same structure, but armed with movable spines borne on tubercles; arms dichotomous, biserial;

stem circular in section. *Dichocrinus*, Münster (1838, W. & Sp., 1897, syn. *Cotyledonocrinus*, Casseday & Lyon, 1860), Carboniferous, Europe and N. America; BB 2; IBr 2, united by syzygy; $\mathrm{IIBr}_{1 \text{ and } 2}$ and, when arms fork again, $\mathrm{IIIBr}_{1 \text{ and } 2}$ are united by syzygy; arms thin, uniserial or biserial, occasionally pendent; stem circular in section. *Camptocrinus*, W. & Sp. (1897), Carboniferous, America, differs from *Dichocrinus* only in the structure of the stem, which in its crescentic section and 2 series of cirri resembles that of *Herpetocrinus* (p. 147). *Talarocrinus*, W. & Sp. (1881-97), Carboniferous, N. America; differs from its ancestor *Dichocrinus* in its more massive plates and in having but one IBr to an arm, and that small; anal resembles ant. R in shape and size; arms branch twice, biserial, free from IIBr inclusive. *Pterotocrinus*, Lyon & Casseday (1859, W. & Sp., 1897; syn. *Asterocrinus*, Lyon *non* Münster), Carboniferous, N. America; a remarkable modification of *Talarocrinus*, with Br up to IIIBr incorporated in cup; large wing-like processes spread out from tegmen, and probably represent the hypertrophied axillary IAmb. With this exaggerated type, the nearest approach to the true Camerata, the Hexacrinidae become extinct. FAMILY 3. ACROCRINIDAE. Cup formed of 2 BB, forming a hexagon; 5 RR; 1 anal in line with RR; and a large belt of accessory plates between BB and RR. *Acrocrinus*, Yandell (1855, W. & Sp., 1897), later Carboniferous, N. America (Fig. LXXIII.); derived from *Dichocrinus*, which it otherwise resembles, by the gradual intercalation of 6-20 circlets of supplementary plates, "superbasals" (SB); the SB immediately above BB are always the latest formed and the smallest; the SB supporting the anal and ant. R are in single series, the rest alternate. In *A. amphora* the arms were recumbent on the cup and apparently immovable. This remarkable family was the last to appear, and survived all other Adunata and all Camerata.

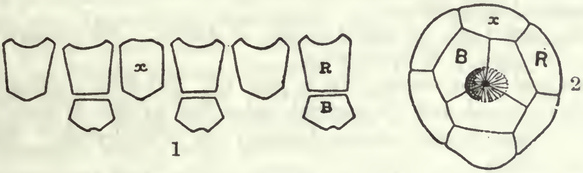


FIG. LXXII

Hexacrinus. 1, analysis of cup; 2, *H. pateraeformis*, cup from below. (After L. Schultze.) × ½.

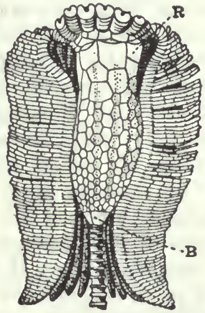


FIG. LXXIII.

Acrocrinus amphora. (Reconstructed from Wachsmuth & Springer.) × ⅓.

ORDER 3. Monocyclica Camerata

(= CAMERATA, W. & Sp. *pars*).

Monocyclica in which IBr, two in each ray (exc. *Stereocrinus*, *Hadrocrinus*, *Alloprosallocrinus*) and often succeeding orders of Br, are incorporated by iBr in the dorsal cup (becoming "fixed brachials," $\overline{\mathrm{Br}}$), while the corresponding Amb are either incorporated in, or pressed below, the tegmen by iAmb; all thecal plates united by suture, somewhat loose in the earliest forms, but speedily becoming close, and producing a rigid theca; mouth and tegminal food-grooves closed; arms pinnulate.

The families may be grouped somewhat after the plan of Wachsmuth and Springer (1897), thus :—

A. No anal plate in radial circlet of patina. BB usually form a pentagon. Melocrinoidea.

B. An anal plate between RR in post. IR. BB form a hexagon.

1. Proximal anal heptagonal, succeeded by one or more in the same vertical series, between the ordinary iBr. Batocrinoidea.
2. Proximal anal hexagonal, succeeded by no vertical series, but by 2 iBr. Actinocrinoidea.

Whether Group *B.* was derived from some genus in Group *A.* is uncertain; representatives of both groups are found in the Ordovician. It is more probable that *B*,2 was derived from *B*,1, by way of the Periechocrinidae. Among Melocrinoidea the Patelliocrinidae are scarcely removed from the Inadunata, and some of their genera might almost be placed with the early Adunata, with which they were contemporary. Although their occurrence in the Ordovician is doubtful, yet the existence of the family points to the path along which the Camerata ascended. The Glyptocrinidae and Melocrinidae, which differ in little but number of BB, and both have anals in the dorsal cup, may have been derived from such a form as *Stelidiocrinus*, which also has anals. With less doubt we infer that the Patelliocrinidae without anals gave rise to the similarly constituted Clonocrinidae, from which sprang Eucalyptocrinidae, and probably also Dolatocrinidae. Among Batocrinoidea the simplest and one of the oldest genera is *Tanaocrinus*, with 5 BB, and not far from it come the earlier Xenocrinidae, with 4 BB, which perhaps led on to Periechocrinidae, and so to Actinocrinoidea. The important ancestral family, however, is the Silurian Carpocrinidae, in which *Acacocrinus* is nearest to the Inadunate type. From them arose *Barrandeocrinus* with its recumbent arms, then the Coeliocrinidae without anal tube or respiratory pores, and, later on, the Batocrinidae possessed of both those structures. No members of this order survived the Lower Carboniferous, but during their history they developed some of the most numerous in individuals and species among crinoid genera, and in *Barrandeocrinus*, *Eucalyptocrinus*, *Agaricocrinus*, and *Strotocrinus*, some of the most remarkable of all Echinoderma.

SUB-ORDER 1. **Melocrinoidea.** Monocyclica Camerata with RR in contact all round; IBr_1 usually quadrangular.

FAMILY 1. GLYPTOCRINIDAE. Melocrinoidea with 5 BB; in each half-ray 2-8 $\overline{\mathrm{IIBr}}$, sometimes $\overline{\mathrm{IIIBr}}$; free arms rarely branch beyond IIIBr, and may be uniserial, zigzag, or biserial; iBr numerous but definite; iIIBr numerous, less definite; a ridge of anals in post. IR; tegmen of numerous small plates; stem round, with pentagonal lumen. All Ordovician of N. America, European representatives doubtful. Genera—

Glyptocrinus, Hall (1847 ; W. & Sp., 1897 ; synn. *Canistrocrinus*, W. & Sp. ; *Pycnocrinus*, S. A. Miller), has small BB and arms in zigzag (Fig. XXV.). *Schizocrinus*, Hall (1847 ; W. & Sp., 1881 ; (?) syn. *Scyphocrinus*, Hall *non* Zenker), doubtful, but close to *Glyptocrinus*, arms uniserial. *Periglyptocrinus*, W. & Sp. (1897), has large BB and biserial arms. FAMILY 2. MELOCRINIDAE. Melocrinoidea with 4 BB ; in each half-ray 2-5 $\overline{\rm IIBr}$; these support 2 or 4 main rami giving off pinnules or pinnulate ramuli ; iBr, iIIBr, and post. IR as in Glyptocrinidae ; tegmen of numerous, small, and irregular plates ; stem round. Genera—*Scyphocrinus*, Zenker (1833 ; *non* Hall, *nec* Pictet), Silurian, Bohemia and (?) N. America. Cup very large, including many of the proximal ramuli, which enter the iBr and iIIBr areas ; subsequent rami are free and divergent ; rami and ramuli uniserial ; root a large hollow spheroid strengthened by internal septa, regarded as a float (= *Camarocrinus*) by Hall, as a cystid (= *Lobolithus*) by Barrande. *Mariacrinus*, Hall (1859, restr. W. & Sp., 1881-97 ; syn. *Zenkericrinus*, Waag. & Jahn), Silurian, Europe, N. America. Free arms composed of wedge-shaped IIIBr, divergent, may or may not bear a few ramuli on their amedian sides (Fig. LXXIV. 1). *Melocrinus*, Goldfuss (1826 ; W. & Sp., 1897 ; synn. *Astrocrinus*, Conrad ; *Turbinocrinus*, Troost ; *Castanocrinus*, and *Cytocrinus*, C. F. Roem. ; *Clonocrinus*, Oehlert), Devonian, Europe and N. America ; the 2 main rami of each arm are laterally fused into one trunk with single large ventral groove ; this bears paired biserial pinnulate ramuli (Fig. LXXIV. 2) ; thus the genus is related to *Mariacrinus* as *Eucladocrinus* (p. 158) to *Platycrinus*, and as *Steganocrinus* (p. 170) to *Actinocrinus*. *Ctenocrinus*, Bronn (1840, em. Follmann, 1887), Lower Devonian, W. Europe, is distinguished by Jaekel (1895), but merged with *Melocrinus* by W. & Sp. (1897) ; the ossicles of the rami are compound, and each may bear 2 pinnules.

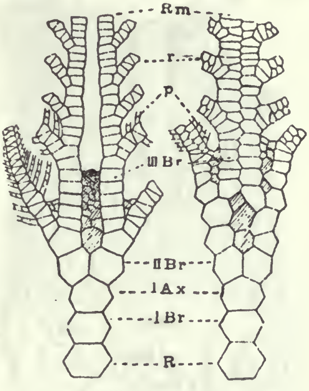


FIG. LXXIV.

Rays of Melocrinidae. 1, *Mariacrinus*, from Brit. Mus. 57475. 2, *Melocrinus nobilissimus* (after Wachsmuth & Springer). *Rm*, ramus ; *r*, ramule ; *p*, pinnule. Supplementary plates are shaded.

FAMILY 3. PATELLIOCRINIDAE. Melocrinoidea with but few Br incorporated in cup ; BB usually 3, unequal, may be the original 5, or may fuse to 1 ; both $\overline{\rm IBr}$ resemble free brachials ; in each half-ray 1, or generally 2, $\overline{\rm IIBr}$, merging into free arms, which may be uniserial, zigzag, or biserial ; iBr 2-6, a single one rests on RR ; stem small and round. This early Palaeozoic family contains genera with and without additional plates in post. IR ; but all are simple forms, scarcely more removed from the Inadunate type than are the Silurian Adunata. They may be intermediate between Inadunata and some more advanced Camerata, *e.g.* Clonocrinidae ; but it is not probable that they represent the ancestors of Glyptocrinidae or Melocrinidae. Genera—*Stelidicorinus*,

Angelin (1878; [?] syn. *Harmocrinus*, Ang.), Ordovician, N. America and Silurian, Gotland (Fig. LXXV. 1, 2); 5 BB, uniserial arms, anals in post. IR, large orals. *Macrostylocrinus*, Hall (1852, W. & Sp., 1897), Silurian, N. America; 3 BB, biserial arms, anals in post. IR, small plates in tegmen. *Allocrinus*, W. & Sp. (1889-97), Silurian, N. America; 3 BB, uniserial arms, no anals in post. IR. *Patelliocrinus*, Angelin (1878), Silurian, Gotland (Fig. LXXV. 3); 3 BB, arms zigzag or biserial, no anals. *Briarocrinus*, Angelin (1878), Silurian, Gotland; 3 BB, arms secondarily uniserial, *i.e.* IIBr are compound plates, anals uncertain. *Centriocrinus*, Bather (1899, nom. mut. pro "*Centrocrinus*," W. & Sp., 1881, *non* Austin, 1843, *nec* Worthen, 1890); BB fused, arms unknown, no anals in post. IR. Family 4. Clonocrinidae. Melocrinoidea with 4 BB; in each half-ray 1-2 IIBr, with varying number of IIIBr and even occasionally IVBr; free arms biserial, sometimes forking as far as VIIBr; iBr few and definite; iIIBr few, not always present; occasional iIIIBr; no anals in post. IR; tegmen unknown; stem round or sub-pentagonal. Genera—*Clonocrinus*, Quenstedt (1876, *non* Oehlert, 1879; syn. *Corymbocrinus*, Ang.), Silurian, England, Gotland, and N. America; base concave; free arms isotomous from IIIBr to VIIBr; iBr in a single vertical row, the two proximal large and definite. This genus leads towards Eucalyptocrinidae. *Polypeltes*, Angelin (1878), Silurian, Gotland, seems to have pinnules incorporated

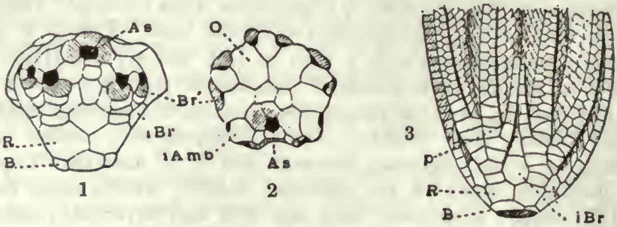


Fig. LXXV.

Patelliocrinidae. 1 and 2, *Stelidiocrinus capitulum*. 1, calyx from posterior; 2, oral surface; 3, *Patelliocrinus pachydactylus*. (All after Angelin, about nat. size.)

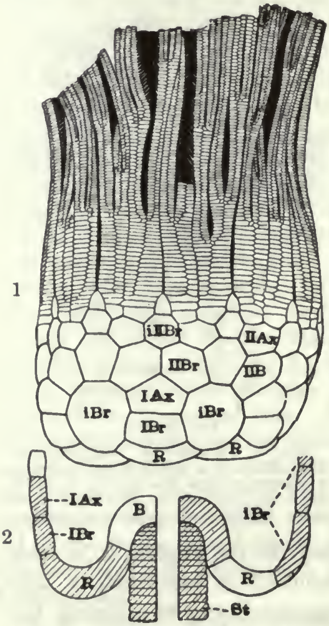


Fig. LXXVI.

Clonocrinus polydactylus. 1, from side (from Brit. Mus. 40257); 2, vertical section (from Brit. Mus. E6489). Lettering as usual. Nat. size.

in the cup. It leads on to *Trybliocrinus*, Geinitz (1867; syn. *Spyridiocrinus*, Oehlert, 1891), Lower Devonian, Germany and France, which also has a concave base. *Technocrinus*, Hall (1859, W. & Sp., 1897), Devonian, Md., U.S.A., base convex, arms not branching beyond IIIBr, no iIIBr; the cup plates have axial folds as in Dolatocrinidae, which family may be thus connected with Corymbocrinidae. FAMILY 5. EUCALYPTOCRINIDAE. Melocrinoidea with usually concave patina of 4 BB and 5 RR; in each half-ray are 2 $\overline{\mathrm{IIBr}}$, supporting $\overline{\mathrm{IIIBr}}_1$ (and in *Eucalyptocrinus* $\overline{\mathrm{IIIBr}}_2$), followed by IIIBr, proximally uniserial, distally biserial; iBr 3, 2 resting on 1; iIIBr 1; tegmen elevated in a central anal tube, and composed of 4 circlets of large plates, variously shaped

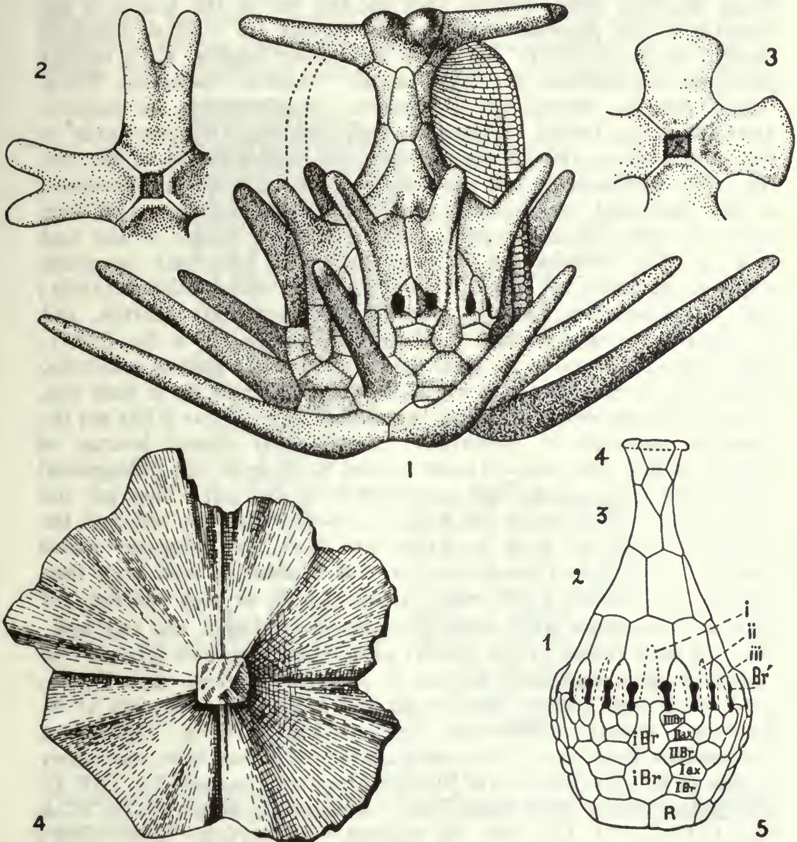


FIG. LXXVII.

Eucalyptocrinidae. 1, *Callicrinus murchisonianus* from the side, arms removed except on the right; 2, plates from distal end of anal tube; 3, the same plates from *C. costatus*; 4, similar plates described by Hall as *Cryptodiscus*; 5, calyx of *Callicrinus costatus*; *1, 2, 3, 4* denote successive circlets of the anal tube; i, ii, iii, denote the areas of origin of interbrachial processes. Other letters as usual. 1, 2, 3, 5, after Angelin; 4, after Hall.

and bearing processes. When stripped of arms and processes, the theca resembles a sherry-decanter with a kick at the bottom. At the junction of cup and tegmen are the 10 pairs of ambulacral openings for food-grooves and associated vessels, which pass beneath the tegmen to a central mouth suspended beneath the neck of the decanter. From this a gut winds dextrally down, around, then up, and out at the mouth of the decanter. The processes borne by the tegmen are vertical partitions rising from the fixed iBr and iIIBr to varying heights, while smaller partitions are between the IIIBr series. Genera—*Callicrinus*, d'Orb. (1849), Silurian, Europe and N. America (Fig. LXXVII., see Angelin, 1878, W. & Sp., 1897). The cup is built on almost the same plan as that of *Clonocrinus*, the difference lying in the vertical fission of the 2nd iBr. The partitions do not rise very high between the arm-branches; on the other hand, large spinous processes are frequently given off from plates of both cup and tegmen, while the upper circlet of the anal tube is often extended in 4 quadrant-shaped horizontal extensions (*Cryptodiscus*, Hall; see Weller, 1898). *Eucalyptocrinus*, Goldfuss (1826; syn. *Hypanthocrinus*, Phillips), Silurian of Europe, N. America, and (?) Victoria, Devonian of Eifel (see Angelin, 1878, and W. & Sp., 1897); differs from *Callicrinus* in the great development of the vertical partitions, which form compartments in which the arms rest right up to their tips, so that the closed crown is almost egg-shaped, especially as it has not the obtrusive ornament of *Callicrinus*. Angelin has figured laminae of stereom within the theca; these served to support the subtegminal food-grooves and mouth, and are pierced by the gut; they are not hydrospires. This family was richer in species than any other of the Silurian; while the main structure was fixed, the ornament varied greatly. FAMILY 6. DOLATOCRINIDAE. Melocrinoidea with large base, flattened or concave, 3 BB, nearly always fused; in each half-ray, 1-4 IIBr, and sometimes IIIBr and IVBr; free arms biserial, and may fork; iBr,3 or more ranges; iIIBr usually present, merging with iIIAmb; an additional iBr exceptionally present in post. IR; tegmen, when known, solid, with large plates; stem round and large. All Devonian of N. America. Genera—*Dolatocrinus*, Lyon (1857; W. & Sp., 1897; syn. *Cacabocrinus*, Hall), has 2 IBr, a stout almost central anal tube, respiratory (?) slits in interbrachial areas at junction of cup with tegmen (Fig. XLV. 1), and plates usually with axial folds. *Stereocrinus*, Barris (1878, W. & Sp., 1897), has 1 IBr, and BB unfused. *Hadrocrinus*, Lyon (1869; W. & Sp., 1897; syn. [?] *Coronocrinus*, Hall), has 1 IBr and large iBr variable in number and arrangement; very large, and imperfectly known. The single primibrachs of *Stereocrinus* and *Hadrocrinus* probably represent the two IBr of *Dolatocrinus* fused (cf. *Alloprosallocrinus*).

SUB-ORDER 2. **Batocrinoidea.** RR in lateral contact except in post. IR. Proximal anal heptagonal. IBr_1 quadrangular, except in Periechocrinidae.

FAMILY 1. TANAOCRINIDAE. Batocrinoidea with 5 BB; the proximal IIBr fixed, but outwardly resemble free brachials; arms fork still further, brachials wedge-shaped; iBr and iIIBr numerous, irregular, occupying depressed areas connected with tegmen, which was probably flexible and composed of small plates; in post. IR is a vertical ridge of anals;

stem relatively large and sub-pentagonal. Genus—*Tanaocrinus*, W. & Sp. (1897), Ordovician, Ohio (Fig. LXXVIII. 1, 2). In structure and in time this genus is well fitted to be taken as an ancestor of the Carpocrinidae. FAMILY 2. XENOCRINIDAE. Batocrinoidea with 4 BB; each half-ray contains $\overline{\text{IIBr}}$, and sometimes $\overline{\text{IIIBr}}$; free arms in zigzag or biserial. iBr and iIIBr, also iIIIBr when present, numerous. Post. IR wider than the others, divided by a longitudinal row of ridged anals. Tegmen of minute irregular plates. Stem quadrangular to circular in section, with pentagonal lumen. Genera—*Xenocrinus*, S. A. Miller (1881; W. & Sp., 1897; Fig. LXXVIII. 3); iBr sink between RR, so as almost to rest on BB; IIBr are finials. *Compsocrinus*, S. A. Miller (1883; W. & Sp., 1897; Fig. LXXVIII. 4), has RR in contact except on anal side; IIIBr sometimes fixed; iBr stouter than in *Xenocrinus*. Both Ordovician, Ohio. *Abacocrinus*, Angelin (1878; syn. ? *Carolicrinus*, Waag. & Jahn), Silurian, Gotland and (?) Bohemia, is more highly developed. Between it and *Compsocrinus* we must imagine a form in which the free Br became biserial, while the free rami forked several times. In *Abacocrinus* the proximal biserial brachials (IIIBr) with their pinnules are incorporated in the dorsal cup; the stem has changed from sub-quadrangular

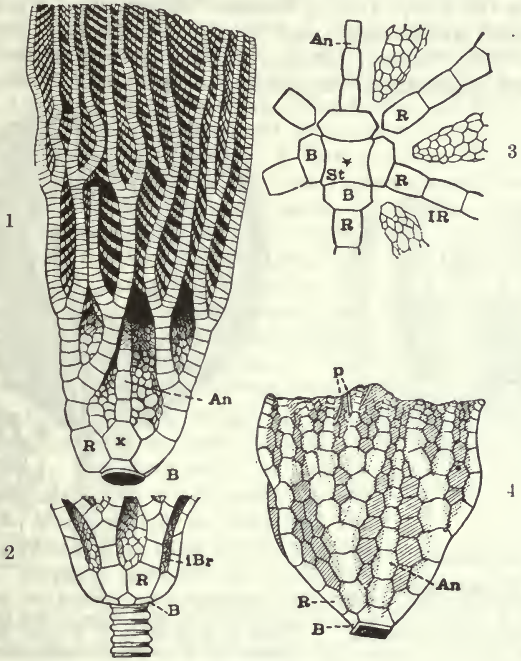


FIG. LXXVIII.

Tanaocrinidae and Xenocrinidae. 1, *Tanocrinus typus*, posterior view, × 2 diam. 2, anterior view, × 2 diam. 3, *Xenocrinus*, analysis of cup. 4, *Compsocrinus harrisi*, cup from posterior, diagrammatic, × 2 diam. (All adapted from W. & Sp.)

to circular, but the columnals still alternate in size. From the imagined intermediate form (not from *Abacocrinus* itself) *Periechocrinus* may have been derived by fusion of 2 BB. FAMILY 3. CARPOCRINIDAE. Batocrinoidea with 3 BB (? fused in *Macarocrinus*); RR rather large; each half-ray contains 1-3 $\overline{\text{IIBr}}$ usually passing into the free arms, which are usually 2, occasionally 3, to each ray; iBr 2-5, in contact with iAmb; iIIBr may be present in limited and definite number; tegmen of numerous small plates, with a few larger ones; in post. IR a vertical row of anals; stem large and round, usually with small pentagonal lumen. Genera—*Acacocrinus*, W. & Sp. (1897), Silurian, Indiana, has 2 arms to each ray; brachials wedge-shaped, each bearing one pinnule. *Desmidocrinus*, Angelin (1878), Silurian, Europe; in each ray one of the rami forks again almost immediately. *Macarocrinus*, Jaekel (1895), Lower Devonian, Eifel, differs in greater length of Br, in fusion of BB, and presence of one $\overline{\text{IIBr}}$ instead of two (Fig. LXXIX. 1). *Carpocrinus*, J. Müller (1841; synn. *Phoenicocrinus*, Austin; *Abracrinus*, d'Orb.; *Habrocrinus*, *Pionocrinus*, and [?] *Leptocrinus*, Angelin, 1878. See W. & Sp., 1881), Silurian, Europe; derived from *Desmidocrinus* by fusion of free Br to form uniserial ossicles each supporting 2 or more pinnules, and by atrophy of the unpaired ramus, which resembles a large proximal pinnule (Fig. LXXIX. 2). FAMILY 4. BARRANDEOCRINIDAE. Batocrinoidea with 3 BB; RR irregularly shaped; each half-ray containing 1 $\overline{\text{IIBr}}$, which supports a free arm, biserial, and recumbent over dorsal cup; iBr, 3, in contact with iAmb; tegmen solid with large sub-spinous O, alternating with 5 radial dome-plates; stem large and round. Genus—*Barrandeocrinus*, Angelin (1878; syn. [?] *Cylicocrinus*, S. A. Miller *non* Müller; see W. & Sp., 1897), Silurian, Gotland and (?) N. America (Fig. LXXX.).

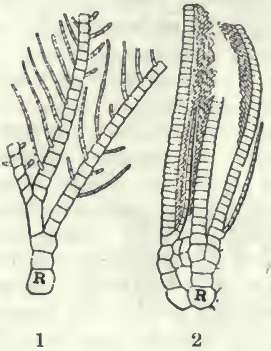


FIG. LXXIX.

Arms of Carpocrinidae. 1, *Macarocrinus Springeri* (after Jaekel). 2, *Carpocrinus simplex* (based on Brit. Mus. 5536 & 57360).

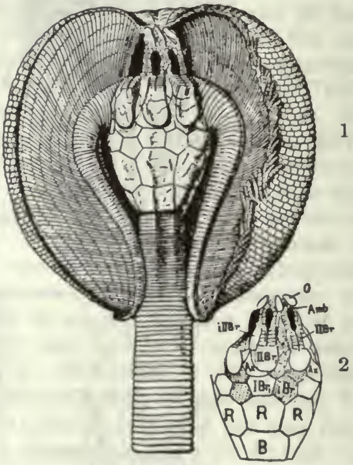


FIG. LXXX.

Barrandeocrinus sceptrum. 1, reconstruction of the crown, with three of the rami removed (after G. Liljevall in W. & Sp.). Nat. size. 2, diagram of the calyx. Lettering as usual.

The chief feature is the fixed recumbency of the arms, as in some Hexacrinidae and *Acrocrinus;* but differing from those forms in that the pinnules were very close-set, and folded in two rolls over the ventral groove when closed. Except for this and the consequently more solid tegmen, the genus is not far removed from the Carpocrinidae. Ant. R is hexagonal; r. and l. ant. RR heptagonal; r. and l. post. RR pentagonal.

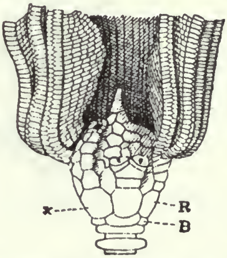


FIG. LXXXI.
Coelocrinus immaturus, from Brit. Mus. E1773. × $\frac{4}{3}$.

FAMILY 5. COELOCRINIDAE. Batocrinoidea with 3 BB; in each half-ray, 1 or 2 $\overline{\text{IIBr}}$; free arms separated by 3 or more iBr in contact with iAmb, 2-4 biserial rami to each ray; a row of anals in post. IR, supporting no tube; but anus opening marginally from a slight prominence; tegmen solid, with large O, esp. post. O; no respiratory pores known. Genera—*Coelocrinus*, Meek & Worth. (1865-66; synn. *Sphaerocrinus*, M. & W. *non* Roem.; *Aorocrinus*, W. & Sp., 1897), Devonian and Carboniferous, N. America, and (?) Devonian, Europe (Fig. LXXXI.). 2 or 4 rami to each ray, each with independent opening into the theca; cup extending below arm-bases. *Dorycrinus*, C. F. Roemer (1854, W. & Sp., 1897), Carboniferous, N. America; derived from *Coelocrinus* with convex base; rami paired, 2 to a single opening; radial dome-plates of tegmen bear large spines. *Agaricocrinus*, Hall ex Troost (1858; W. & Sp., 1897), Carboniferous, N. America; derived from *Coelocrinus* with concave base, that feature being greatly exaggerated so that the cup does not project below the arm-bases; rami 2-4 in each ray, each with independent opening. FAMILY 6. BATOCRINIDAE. Batocrinoidea with 3 BB; each half-ray contains 1-5 $\overline{\text{IIBr}}$, also $\overline{\text{IIIBr}}$, 1-5, always in adanal series, and sometimes in the rest, but rarely in anterior series; free arms with 1-4 biserial rami in each ray; iBr, 1-15, usually unconnected with iAmb, except in post. IR, and sometimes separated from them by the brachials there also; plates in posterior IR 2-19, perhaps more; anal tube long, usually stout, and central; tegmen solid, with O and radial dome-plates usually prominent, post. O always pronounced; 10-20 respiratory pores characteristic (Fig. XLV. 2), but doubtful in *Dizygocrinus* and very doubtful in *Hyperocrinus;* stem round, usually stout, with small pentagonal lumen. The family is confined to the Lower Carboniferous rocks of central N. America, where it flourished exuberantly along with the parallel family Coelocrinidae. *Batocrinus* came first (Kinderhook) and went last (St. Louis); the rest are confined to Burlington and Keokuk Groups. Genera—*Batocrinus*, Casseday (1854; em. W. & Sp., 1897), has 1-3 iBr separated from iAmb by IIIBr; 18-26 short arm-rami set regularly round periphery (Fig. LXXXII.). *Eretmocrinus*, Lyon & Casseday (1859; W. & Sp., 1897), like *Batocrinus*, but has 12-26 long paddle-shaped arm-rami, and eccentric anal tube. *Alloprosallocrinus*, Ly. & Cass. (1860, W. & Sp., 1897), constructed like *Batocrinus*, but converges in outward shape towards *Agaricocrinus*. *Eutrochocrinus*, W. & Sp. (1897), 18-40 short rami, set regularly around periphery like spokes of a wheel; iBr may or may not join iAmb; iIIBr often present. *Dizygocrinus*, W. & Sp. (1897), like *Eutrochocrinus*, but with rounded calyx, more variable in composition, anal tube and stem rather slender. *Hyperocrinus*, Meek & Worthen (1865, as *Uperocrinus;* syn. *Lobocrinus*, W. & Sp., 1897); 18-22 free rami, arranged in arm-groups, separated by iBr which join iAmb; iIIBr sometimes present; lofty tegmen; respiratory pores unknown. *Macrocrinus*, W. & Sp. (1897); 12-16 rami, in groups, but not separated by iBr except in post. IR; anal tube tapering; stem slender; tegmen conical or hemispherical; respiratory pores, 10. The study of the relations between these genera is a fertile and unappropriated field.

FAMILY 7. PERIECHOCRINIDAE. Batocrinoidea with 3 BB; $\overline{\mathrm{IBr}}_1$ hexagonal; each half-ray contains 1-5 $\overline{\mathrm{IIBr}}$, and sometimes 2-6 $\overline{\mathrm{IIIBr}}$; free arm-rami biserial, usually branching; iBr numerous and merging into iAmb; post. IR wide, with plates in successive rows of 1, 3, 4-6, etc.; tegmen of numerous small plates in which O, Amb, and radial dome-plates are sometimes to be distinguished, especially post. O; anus without tube, from sub-central to marginal; stem large, round, with wide lumen, round or 5-lobed. Members of this family, esp. *Gennaeocrinus*, are liable to be confounded with Actinocrinidae, but differ in the presence of 3 plates (not 2) in the second row of post. IR, in which respect they resemble Xenocrinidae, Carpocrinidae, Coelocrinidae, and Batocrinidae. Genera—*Periechocrinus*, Austin (1843; synn. *Geocrinus*, d'Orbigny; *Saccocrinus*, Hall ex Troost; *Pyxidocrinus*, J. Müller, *pars*; [?] *Trochocrinus*, Portlock and [?] Pander; [?] *Pradocrinus*, Verneuil, 1850; see W. & Sp., 1897), Silurian to Carboniferous, Europe, N. America, Australia; elongate cup of thin long plates, usually with axial folds, and depressed theca in which O are not distinguishable; arms fork and are less advanced than in *Abacocrinus* (p. 165). *Beyrichocrinus*, Waag. & Jahn (1899), Silurian, Bohemia, little known. *Megistocrinus*, Owen & Shumard (1852; W. & Sp., 1897), Devonian and Carboniferous, N. America, (?) Carboniferous,

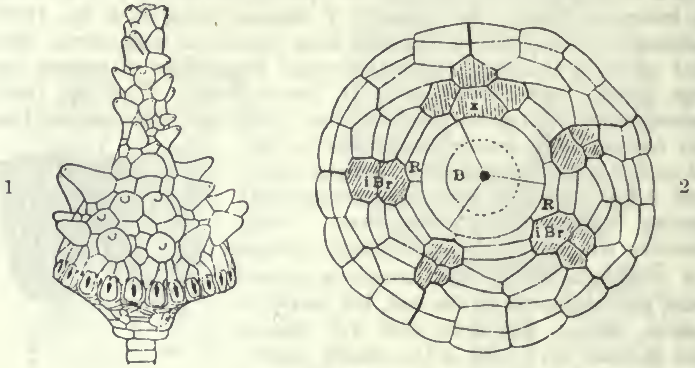


FIG. LXXXII.

Batocrinus. 1, *B. icosidactylus*, calyx from the side (after Casseday, nat. size). 2, cup seen from aboral side, from Brit. Mus. E5055. Supplementary plates shaded. × $\frac{2}{1}$.

England; globose cup of heavy short plates, with tegmen from flat to conical; O, radial dome-plates, and Amb usually distinguishable (Fig. XLII.); free rami grouped in pairs, have covering-plates and side-plates. *Gennaeocrinus*, W. & Sp. (1881-97), Devonian, N. America; low cup of thin plates with axial folds; theca rather depressed and lobed in arm regions; O small but visible, as also are Amb; rami, 8 to a ray, branch from alternate sides of arms; in form like the Actinocrinid *Physetocrinus*.

SUB-ORDER 3. **Actinocrinoidea.** RR in lateral contact except in post. IR; proximal anal hexagonal; IBr$_1$ usually hexagonal; BB 3 equal, forming a hexagon.

FAMILY 1. ACTINOCRINIDAE. Cup conical or bowl-shaped, with ornament of axial folds; only 1 IIBr, which is axillary; free arm-rami branch on alternate sides of the half-rays, starting either from Iax or IIax; all free portions of arms are biserial; proximal pinnulars bear hooks; iBr numerous, primitively merge into iAmb, but become separated therefrom by development and lateral contact of fixed brachials; post. IR wide, with proximal anal followed by 2 plates in second row; tegmen solid; O not prominent, but usually distinguishable; iAmb may cover the tegminal Amb; anus either on a tube or piercing tegmen, either central or eccentric; stem round, with small 5-lobed lumen. The family is confined to the Lower Carboniferous, and flourished chiefly in N. America. *Actinocrinus*, with its descendant *Steganocrinus*, and *Cactocrinus*, with its descendant *Teleiocrinus*, form a group characterised by a long anal tube. In *Physetocrinus* and its descendant *Strotocrinus* the anus pierces the tegmen directly. For complete account of the family and revision of genera see W. & Sp., 1897. Genera—*Actinocrinus*, Miller (1821; synn. *Amphora*, Cumb.; *Blairocrinus*, S. A. Miller; Fig. LXXXIII.); cup-plates with axial folds and parallel ridges; theca lobed at arm-regions, the numerous iBr being depressed, while the higher orders of Br with their Amb form 5 broad rays, sometimes including some iBr; these rays fork and give off free rami to alternate sides every second or third plate, first on outer side from IIax, then on inner side from IIIax, and so on; the rami may branch again; pinnules long, the proximal pinnulars armed with a small hook projecting from the middle; tegmen solid, rising centrally into a stout tube with

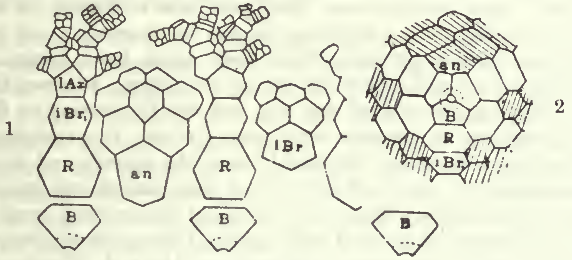


FIG. LXXXIII.

Actinocrinus. 1, analysis of part of cup, showing post. and r. post. interradii. 2, cup from below; the supplementary plates shaded.

anus at distal end; O small and eccentric; Amb visible in tegmen, either as two rows of large covering-plates which pass out from between O and follow the branching of the food-grooves, or as large single plates (IAmb and IIAmb), succeeded by small covering-plates, which pass on to the free arms. *Steganocrinus*, Meek & Worthen (1866), differs from *Actinocrinus* in the extension of each ray into 1 or 2 rigid tubular rami, from which biserial ramuli are given off alternately on opposite sides, either from every ossicle or from every other; covering-plates consist of side-pieces and spinous Amb. *Cactocrinus* (W. & Sp., 1897) differs from *Actinocrinus* in having the arm-rami given off in a continuous row around the theca, the brachials meeting laterally, so that iBr are not in contact with iAmb (*cf. Eutrochocrinus*); bifurcation takes place on each successive plate, *i.e.* all Br, except the finials, are axillary; all pinnulars, except the extreme distal ones, bear hooks which imbricate over the adjacent pinnules (*cf.* structure of a feather); covering-plates consist of side-pieces and Amb; Br and tegminal plates spinous (cf. Fig. XLIV.). *Teleiocrinus*, W. & Sp. (1881; syn. *Calathocrinus*, Hall, *pars*, *non* v. Meyer); a modified *Cactocrinus* in which the arms have become so numerous and crowded that they are pushed outward, while their bases have become united and extended as a broad rim at the top of the theca; between the Amb and iAmb forming the roof of this rim, and the Br forming its floor, are developed processes of stereom serving as girders; the ambulacra with their ambulacrals are mostly depressed below the tegmen and covered by iAmb; a respiratory pore is at the side of each ambulacral opening into the theca. *Physetocrinus*, Meek & Worthen (1869), differs from *Actinocrinus* in the absence of an anal tube, and in bifurcation of arms on each successive Br, as in *Cactocrinus*. *Strotocrinus*, Meek & Worthen (1866), often confounded with *Teleiocrinus*, towards which it is convergent, bears to *Physetocrinus* precisely the same relation as *Teleiocrinus* bears to *Cactocrinus*. *Sampsonocrinus*, Mill. & Gurl. (1895), Carboniferous, Missouri, has r. and l. post. iBr truncating BB, and only 1 IBr in r. and l. ant. radii; the unique specimen is best regarded as an abnormal *Actinocrinus*. Compare *Phillipsocrinus*, M'Coy (1844 or 1862), Carboniferous, Ireland, in which also some iBr truncate BB; but since BB are here 4, this may be a more direct descendant of Xenocrinidae, perhaps by way of the Silurian *Laubeocrinus*, Waagen & Jahn (1899), which seems a link between early Batocrinoidea and Actinocrinoidea. FAMILY 2. AMPHORACRINIDAE. Actinocrinoidea with cup depressed and tegmen much elevated, accompanied by downward projection of proximal regions of arm-rays; cup-plates with granulo-vermicular ornament; iBr few; in other respects like Actinocrinidae. Genus—*Amphoracrinus*, Austin (1848), Carboniferous, Europe and N. America; arms free from Iax or $IIBr_1$; anal tube short and eccentric. Two American species occasionally have 3 plates (instead of 2) succeeding the proximal anal, but the middle of these is small and wedge-shaped, barely touching the anal; this may be a plate of the ensuing row pressed down, or it may represent the middle plate in Batocrinoidea.

SUB-CLASS 2. DICYCLICA, Bather (1899).

Crinoidea in which the base consists of BB and IBB, the latter being liable to atrophy or fusion with the proximale, but the aboral prolongations of the chambered organ are always radial; new columnals may or may not be introduced at the proximal end of the stem.

ORDER 1. **Dicyclica Inadunata**

(= INADUNATA, W. & Sp. *pars*, *emend.*).

Dicyclica in which the dorsal cup primitively is confined to the patina and occasional intercalated anals, and no other plates ever occur between RR (Grade: Distincta); Br may be incorporated in the cup, with or without iBr, but never rigidly, and their corresponding Amb remain supra-tegminal (Grade: Articulata); new columnals are introduced at the extreme proximal end of the stem.

This order, so far as its Palaeozoic genera are concerned, corresponds roughly to the Inadunata Fistulata of Wachsmuth & Springer, and entirely to the Inadunata Dicyclica of Bather with an error or two corrected; but it includes also some of Müller's Articulata and some of Wachsmuth & Springer's Larviformia. The latter authors have themselves proved the connection of the Encrinidae and Pentacrinidae with their Fistulata. The distribution of the 70 genera into families would present no great difficulty, were a purely morphological classification our aim. One might use, as has been done, such characters as the presence or absence of pinnules, of an anal tube, of a radianal, of articulation between cup-plates, or of simply bifurcate as contrasted with dichotomous arms. But there is every gradation in the development of these characters, pinnulate forms being derived from non-pinnulate, the radianal gradually disappearing, articulation of plates developed as need arose, and so on. Hence the great division into Cyathocrinidae and Poteriocrinidae (W. & Sp., 1886; Zittel, 1895) cannot meet the needs of the phylogenist. An attempt to sketch the actual race-history (Bather, 1890) resulted in the recognition of a distinction between *Dendrocrinus* and its allies, with their broad radial facets and thin tegmen on the one hand, and *Cyathocrinus* and its allies, with narrower facets and more solid tegmen on the other, while the pinnulate forms were all derived from the Dendrocrinidae. This distinction, subsequently strengthened (Bather, 1893), has been made much of by Jaekel (1895), who divides all his Fistulata into Cyathocrinacea, Dendrocrinacea, and Poteriocrinacea, the last group being derived from the Dendrocrinacea, and giving rise to the Articulata (Jaekel). It is therefore but a slight step to establish two sub-orders, Dendrocrinoidea and Cyathocrinoidea. Of these the latter were the first to be specialised and the first to disappear. The Dendrocrinoidea moved more slowly and went further—even to our own day—undergoing modification in the development of the anal tube, in the pinnulation of the arms, and in the relation of arms to cup. Moreover, from them branched off the order Flexibilia, probably on more than one occasion.

Sub-Order 1. **Cyathocrinoidea.** Dicyclica Inadunata, with a fairly stout tegmen, in which 5 orals (Δ, sub-ambulacrals, interradials, consolidating apparatus, of authors) are usually conspicuous, helping to stiffen the tegmen, supporting the ambulacra on their adjacent edges, and enclosing but not covering the peristome; post. O frequently a madreporite; radial facet usually narrow; arms distinct from dorsal cup, unbranched or dichotomous; none attain the pinnulate stage, but the presence of pinnules would not in itself remove a genus from the sub-order.

Family 1. Carabocrinidae. Cyathocrinoidea with one or more large anals in line with RR; RA supporting these, and resting on a supplemental plate intercalated between post. B and r. post. B and resting on IBB. Anus, surrounded by a few small plates, pierces tegmen between x and post. O. Strong stereom-folds pass across the radio-oral sutures. Post. O pierced by hydropore (a madreporite). Arms stout and short. Genera—*Carabocrinus*, Billings (1856,-59); *Strophocrinus*, Sardeson (1899), both Ordovician, N. America (Fig. LXXXIV.). The radio-oral folds are probably vestigial hydrospires (cf. *Hybocrinus*). The interradial tegminal plates are admittedly homologous with orals, and ambulacrals rest on their apposed edges (as in Fig. V. 2; see also p. 126).

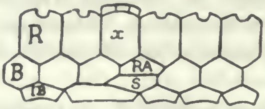


Fig. LXXXIV.
Analysis of cup of *Carabocrinus*.

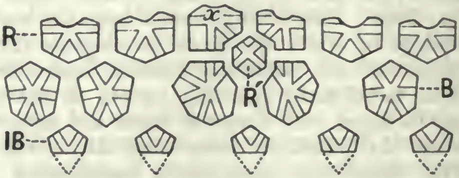


Fig. LXXXV.
Analysis of cup of *Palaeocrinus*, showing the axial folds of the plates. *R'* radianal.

Family 2. Palaeocrinidae. Cyathocrinoidea with anal x in line with RR; RA smaller and rhomboidal, abutting on x and not separating r. post. Rs from r. post. B; anal tube slightly developed; 5 O surround a pentagonal peristome; post. O a madreporite; arms narrow, rising from well-defined facet, axial canal not separate from ventral groove, but passes into thecal cavity through a large opening between R and adjacent O. Genera—*Palaeocrinus*, Billings (1859), Ordovician, Canada (Fig. LXXXV).; usually regarded as a synonym of *Dendrocrinus*, to which it is closely allied; but it differs in shape of RA, the defined radial facet, the anal tube composed of but 4 or 5 vertical rows of plates, and above all, the solid orals supporting ambulacrals,—differentiae which place it in this sub-order. Stem shows 5 radial sutures; cup-plates usually folded; arms isotomous to IVBr. *Porocrinus*, Billings (1856-59; see J. Grant, 1881, and Beyrich), Ordovician, Canada and Russia (Fig. LXXXVI.); arms unbranched. Deep folds lie at the angles of all thecal plates, directed towards the angle, and not passing at right angles across the middle of the sutures, thus differing from hydrospires of Eublastoidea and from pectinirhombs; Beyrich imagined them to be separated by suture from the rest of the plate, and Grant described a membrane [?a film of epistereom] covering them. *Bactrocrinus*, Schnur in Steininger (1849), Devonian, Eifel; usually made a synonym of *Homocrinus*, but separated by Zittel (1879), Bather (1893), and Jaekel (1895); differs from *Palaeocrinus* only in the occasionally wider radial facet and rather more developed anal tube, in which points it approaches *Homocrinus*. FAMILY 3. EUSPIROCRINIDAE. Cyathocrinoidea with anal *x* hexagonal or heptagonal, resting on post. B, but rising above level of RR; with RA pentagonal, resting on post. and r. post. BB, supporting *x* on one side, r. post. Rs on the other, and a plate of the anal tube (*rt*) sunk into the cup between them; anus at end of a massive anal tube; post. O a madreporite; arms dichotomous, axial canal not separate from ventral groove. Genera—*Euspirocrinus*, Angelin (1878; see Bather, 1893), Ordovician of Canada, Silurian of Gotland (Figs. LXXXVII. and XXXVIII.). The usual text-book figure of *E. spiralis* is reversed. *Closterocrinus*, Hall (1852), and *Ampheristocrinus*, Hall (1882), both Silurian, N. America; 3 IBB; imperfectly known (Fig. LXXXVIII.). The anal area of the family resembles that of the advanced Dendrocrinoidea. FAMILY 4. SPHAEROCRINIDAE. Cyathocrinoidea, with 3 anal plates as in *Euspirocrinus*, but differing in that RA is comparatively large, *x* not rising above RR, *rt* small and not, or hardly at all, rising above RR; post. O a madreporite; arms isotomous; axial canal separate in Br and R. Genera—*Sphaerocrinus*, C. F. Roemer (1851; for history see Bather, 1892; for structure, Jaekel, 1895), Devonian, Germany and England; the anus pierces the tegmen directly through a ring of small plates. *Parisocrinus*, W. & Sp. (1879), Devonian of Germany, Carboniferous of England and N. America (Fig. XXVI. 6), has a well-developed anal tube of hexagonal plates, which are folded at the edges.

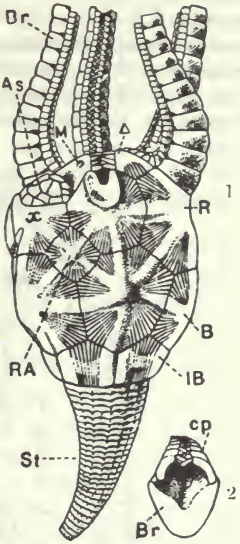


FIG. LXXXVI.

Porocrinus Smithi. 1, partial reconstruction, seen from right posterior radius, the arm of which is removed. Length of stem and arms unknown. (Based on specimens belonging to Dr. G. J. Hinde.) × 2 diam. 2, optical section across a brachial (*Br*), showing relations of covering-plates (*c.p*). × 4 diam. Other lettering as usual.

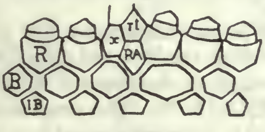


FIG. LXXXVII.

Analysis of cup of *Euspirocrinus spiralis*.

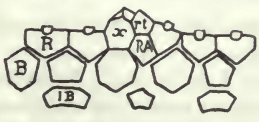


FIG. LXXXVIII.

Analysis of cup of *Ampheristocrinus*.

FAMILY 5. CYATHOCRINIDAE. Cyathocrinoidea, with no anal except *x*, which is in line with RR, and usually supports a large tube; post. O a madreporite; arms isotomous, axial canal separate or not. Genera—*Cyathocrinus*, Miller (1821; see Bather, 1892-93, for full revision and details), Silurian to Carboniferous, world-wide. This, being the best known genus of the sub-order, demands closer description. The dorsal cup (analysed in Fig. LXXXIX. 5) consists of: 5 equal IBB; 5 large BB, all hexagonal except post. B, which is truncate above; 5 shield-shaped RR, each with a facet usually $\frac{1}{2}$ width of plate, the articular surface being either smooth and imperforate, or having a slight transverse ridge pierced by the axial canal (Fig. LXXXIX. 2); a square anal x, in line with RR and resting on truncate post. B. Tegmen consists of 5 O resting on the incurved shoulders of RR, and surrounding a pentagonal peristome (Fig. XXXIX. 1); post. O being large, conspicuous, and pierced by numerous water-pores, the other O being smaller and often almost entirely hidden, partly by ambulacrals resting on the apposed edge of all O, partly by small interambulacrals (Fig. XXXIX. 2). The proximal Amb meet over the peristome and often grow to a large size, sometimes fusing and simulating orals (for which elements they are taken by W. & Sp., see Fig. XLIII.). The anal tube consists of more or less hexagonal plates, arranged in fairly regular longitudinal rows; it varies greatly in width, length, and width of lumen; the anus is at its distal end; the plates may be slightly folded, but are not transversely elongate, nor are there pores,

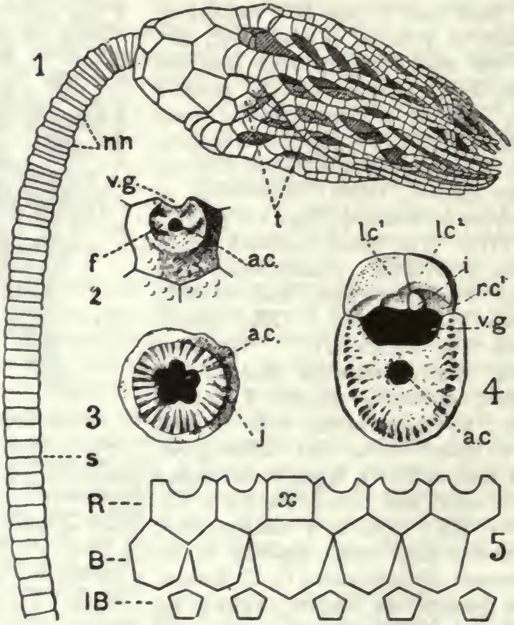


Fig. LXXXIX.

Cyathocrinus. 1, *C. multibrachiatus*, seen from posterior. (Brit. Mus. E5462.) 2, radial of *C. visbycensis*, showing articular facet, × 2. 3, joint-surface of columnal of *C. acinotubus*, × 2. 4, joint-surface of a brachial of same, with covering-plates in position, × 9. 5, analysis of the cup. *a.c*, axial canal; *f*, fulcral ridge; *i*, intercalated plate; *j*, joint-surface; *l.c*^{1} and *l.c*^{2}, the two halves of a covering-plate of the left side; *nn*, nodals; *r.c*^{1}, proximal half of a covering-plate of the right side; *t*, anal tube; *v.g*, ventral groove. (2-5 after Bather.)

or even the appearances of pores, between them (Fig. XXVI. 5). Arms dichotomise 5-7 times, and in each series there are more brachials in the admedian branch of the dichotom (Fig. LXXXIX. 1). The covering-plates are well developed; in their simplest form they are conical, in both outline and longitudinal section, regularly alternating, and each reaching about $\frac{3}{4}$ across the ventral surface; each covering-plate may, however, be transversely divided, and the parts may come to be arranged in a manner too complicated for description here (Fig. LXXXIX. 4). Stem round, with lumen usually 5-lobed; stem and lumen vary in width; columnals low, usually alternating in thickness and height, the smaller ones being those last formed; joint-surface radiately striate (Fig. LXXXIX. 3); no longitudinal sutures and no cirri. *Gissocrinus*, Angelin (1878; em. Bather, 1893), Silurian, Europe and possibly America (Fig. XC.; see also Figs. VIII., IX., and XLI.); connected with *Palaeocrinus;* one or two pairs of IBB usually fuse; cup-plates have clear axial ridges; distal margins of Br usually project; anal tube compressed antero-posteriorly, its plates transversely elongate and folded. *Arachnocrinus*, Meek & Worthen (1866), Silurian to Devonian, America and Europe; small cup and heavy arms, which, together with anal tube, spread out horizontally from the cup. *Lecythocrinus*, Müller (1858, em. Zittel, 1879 = *Taxocrinus briareus*, Schultze, 1866), Devonian, Eifel; stem subquadrangular, with one large central and 4 smaller peripheral canals (cf. Cupressocrinidae). Family 6. Petalocrinidae. Cyathocrinoidea without x in dorsal cup, and with arms fused into solid arm-fans. Genus—*Petalocrinus*, Weller (1896), Silurian, Gotland and N. America, appears to have been derived from *Arachnocrinus* by lateral fusion of the rami of each arm to form a blade

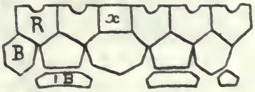


Fig. XC.
Analysis of cup of *Gissocrinus.*

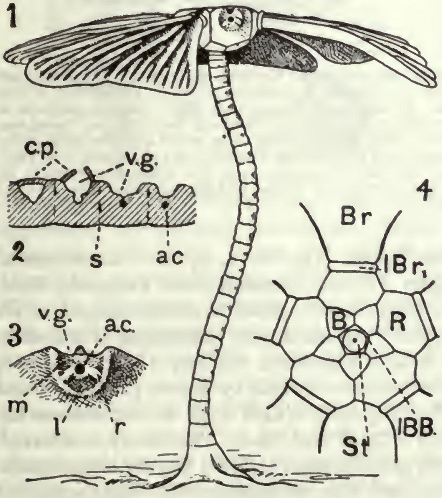


Fig. XCI.

Petalocrinus. 1, partial reconstruction of *P. mirabilis*, with one arm removed to expose radial facet, and other arms devoid of covering-plates; the root is imaginary, × 2 diam. 2, section across four grooves of an arm-fan, showing traces of the original sutures (*s*) between them, covering-plates (*c.p*) closed and open, also stages in the separation of the axial canal (*a.c*) from the ventral groove (*v.g*), compare Fig. VIII., × 5 diam. 3, articular facet of arm-fan of *P. visbycensis;* *m*, muscle-fossa; *l*, dorsal ligament-fossa; *r*, fulcral ridge, × $\frac{8}{3}$. 4, dorsal view of cup and proximal regions of arms of *P. mirabilis;* *Br*, arm-fan; *St*, proximal columnal; other letters as usual, × 3 diam. (3 and 4 are after Bather.)

or fan articulated to the R by a single IBr (Fig. XCI., see Bather, 1898). **Family 7. Crotalocrinidae.** Cyathocrinoidea with cup as in *Cyathocrinus;* anal tube when present constructed like that of *Gissocrinus;* tegmen almost entirely composed of Amb, some of which are much modified; the orals seem to have been covered by these and to have atrophied, except post. O, which remains as a conspicuous plate, apparently madreporic (Fig. XCII. 3); the entry of Amb into the tegmen is connected with the shortening up of proximal portions of arms, so that IBr, IIBr, IIIBr, and sometimes IVBr, all partially rest on R, and are firmly united by suture with it (Fig. XCII. 1). Arms repeatedly isotomous; axial canal distinct, except sometimes in extreme distal region. Stem large, round, with wide lumen (Fig. L. 1, 3, 4). All Silurian. Genera—*Enallocrinus*, d'Orbigny (1850), Gotland and England; arm-branches distinct, often with a pronounced cornice at distal margins of Br (Fig. XCII. 2), in this as in other respects closely resembling *Gissocrinus. Crotalocrinus*, Austin (1842; syn. *Anthocrinus*, Müller, 1853), Gotland, England, and N. America; arm-branches united by lateral processes from each Br, so as to form a flexible network, which may be continuous all round the crown, or divided into 5 broad arm-fans. The family is referred to the Camerata by Wachsmuth and Springer (1888); but the resemblance to *Marsipocrinus* is homoplastic, and the connection with Cyathocrinidae scarcely admits of question. The Crotalocrinidae might be called the Adunata of the Dicyclica, just as *Platycrinus* and its allies are of the Monocyclica. **Family 8. Codiacrinidae.** Cyathocrinoidea with no anal

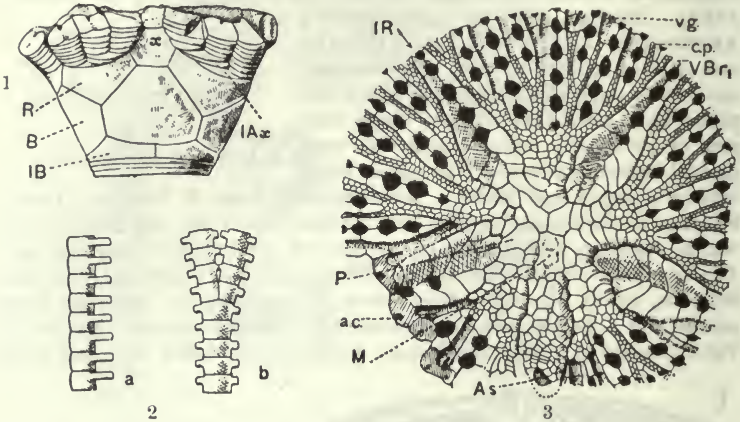


Fig. XCII.

Crotalocrinidae. 1 and 2, *Enallocrinus scriptus* (after Wachsm. & Spr.). 1, posterior view of cup and arm-bases. 2, enlarged view of more distal portions of arms; *a* from side, *b* from back, showing cornice-like projections. 3, tegmen of *Crotalocrinus pulcher*, from a specimen at Stockholm. The arm-branches are united by the lateral processes of the brachials, the spaces between being represented in solid black; the interradii (IR), along which adjacent arms unite, appear as five depressed lanceolate areas, in the posterior of which lies the short anal tube (*As*); the axial canals (*a.c*) are separate from the ventral grooves (*v.g*); the latter are protected by covering-plates (*c.p*), which become larger towards the centre, and four proximal ones (P) meet around the madreporite (M), × 2 diam.

plates in dorsal cup ; with dichotomous arms relatively slightly developed. Genera—*Codiacrinus*, Schultze (1867 ; Follmann, 1887), Devonian, Germany (Fig. XCIII.). *Lecythiocrinus*, White, (1880), Coal Measures of Illinois and Kansas. Both genera little known ; *Codiacrinus* is compared by Schultze with *Myrtillocrinus*, by W. & Sp. with *Achradocrinus*.

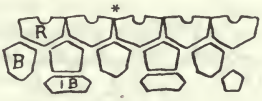


FIG. XCIII.

Analysis of cup of *Codiacrinus Schultzei*. * shows position of anus.

FAMILY 9. CUPRESSOCRINIDAE. Cyathocrinoidea with no anal plates in dorsal cup ; anus piercing tegmen ; arms unbranched (or [?] forking few times) ; stem square in section, with an axial and 4 peripheral canals (cf. *Lecythocrinus*, p. 175). Genera—*Cupressocrinus*, Goldfuss (1826 ; synn. *Halocrinus* & *Cypellocrinus* of Steininger ; see W. & Sp., 1886, and Neumayr, 1889), Devonian, Germany and England (Fig. XCIV.). A massive form with basin-shaped cup ; IBB fused (by some held to be a proximale, Fig. XCIV. 3) ; a stout arm, composed of a few large Br in single series, rests on a facet the full width of each R ; large ambulacrals cover the arm-grooves and are taken for pinnules by Zittel ; the solidity of the close-fitting arms renders a plated tegmen unnecessary, but the 5 orals characteristic of Cyathocrinoidea are retained as a frame ("consolidating apparatus" of authors) around the ventral surface of the cup, post. O being larger than the others and pierced for the rectum (Fig. XCIV. 2).

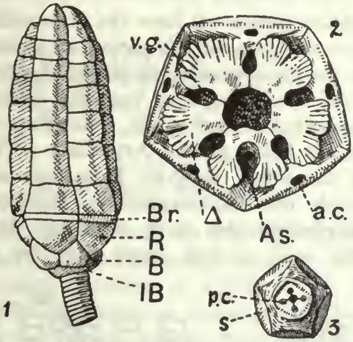


FIG. XCIV.

Cupressocrinus (after L. Schultze). All two-thirds nat. size. 1, *C. inflatus*, complete crown. 2, *C. abbreviatus*, ventral surface of calyx, slightly modified ; shows "consolidating apparatus" of five plates (Δ), here regarded as orals, between which are the passages (*v.g*) for organs of the ventral groove other than the food-groove ; *a.c*, axial canal of radial ; *As*, passage for rectum. 3, infrabasal circlet of same, from below, showing sutural surfaces (*s*) for basals, axial canal, and peripheral canals (*p.c*).

Myrtillocrinus, Sandberger (1855, syn. *Ancyrocrinus*, Hall, see p. 134, Fig. LI.), Devonian, Germany, and N. America ; may have closer affinities with Gasterocomidae. FAMILY 10. GASTEROCOMIDAE. Cyathocrinoidea with anus in side of cup, at a level varying with the genus, either above or below *x*, which is always within limits of cup. Arms apparently small, borne on a narrow horseshoe-shaped facet, with distinct axial canal. O for most part covered by Amb, post. O a large madreporite. IBB small, often fused into 3 plates or 1. Stem usually of Cupressocrinid type. Genera—*Gasterocoma*, Goldfuss (1839, W. & Sp., 1886 ; Jaekel, 1895 ; synn. *Epactocrinus* and *Ceramocrinus*, J. Müller, 1855), Devonian, Germany ; anus below *x*, which is in line with RR ; IBB fused into one. *Nanocrinus*, J. Müller (1856, Schultze, 1867), Devonian, Eifel ; like

Gasterocoma, but ant. R small, without facet; r. ant. R with 2 facets. *Scoliocrinus*, Jaekel (1895), Devonian, Eifel; still more bilateral, in that ant. and l. ant. RR are larger than the rest, and alone bear arms; anus below r. post. R, and x between post. B and r. post. B. *Achradocrinus*, Schultze (1867), Devonian, Eifel (Fig. XCV.); x below anus, and resting on post B; IBB 5; stem round, with single canal. *Hypocrinus*, Beyrich (1864), Carboniferous, Timor; differs from *Achradocrinus* in having IBB fused to 3; referred by most authors to Cystidea Aporita.

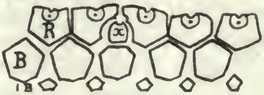
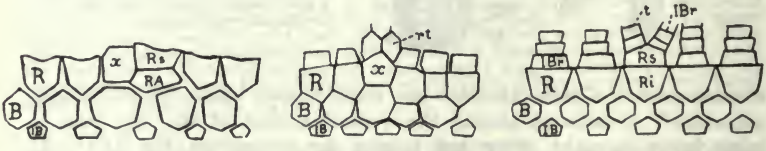


Fig. XCV.
Analysis of cup of *Achradocrinus ventrosus.*

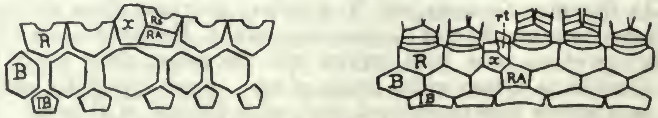
Sub-Order 2. **Dendrocrinoidea.** Dicyclica Inadunata with a thin flexible tegmen, or with the ventral surface almost entirely occupied by a large anal tube or ventral sac (the latter name being needed if the extension contained more than the mere rectum); orals inconspicuous or entirely atrophied in the adult; no madreporite; radial facet often wide, so that the distinctness of arms from dorsal cup is not maintained; arms dichotomous, the dichotomy often irregular, leading up to a pinnulate stage.

Whereas the genera of the Cyathocrinoidea all have the arms either quite distinct from each other above the level of the patina, or at least not united by supplementary plates, the Dendrocrinoidea gradually attain a stage of development in which the arms are thus partially united. Below this stage we may draw a somewhat arbitrary line, separating the former as a grade, Distincta, from the latter grade—Articulata. This line happens to correspond with the break between Palaeozoic and Mesozoic time. We deal first with the Dendrocrinoidea Distincta.

Family 1. Dendrocrinidae. Dendrocrinoidea with regularly dichotomous, non-pinnulate arms, with anal x, and large RA in its primitive position as inferradial (Fig. XCVI.); stem quinquepartite. Genera—*Merocrinus*, Walcott (1883), Ordovician, N. America and England, resembles *Iocrinus* (p. 145) in all but the presence of IBB; anal tube supported by the left shoulder of r. post. Rs. *Ottawacrinus*, W. R. Billings



Merocrinus. *Ottawacrinus.* *Dendrocrinus.*



Homocrinus. Fig. XCVI. *Thenarocrinus.*
Dendrocrinidae. Analyses of cups.

(1887), Ordovician, Canada; *x* rests on post. B, RA immediately above r. post. B; r. post. R*s* is above general level of RR and may be IBr_1. These two genera suggest that RA of Dicyclica may not be strictly homologous with RA of Monocyclica. *Dendrocrinus*, Hall (1852), Ordovician and Silurian, N. America; large anal sac with folded plates making wide anal area in cup (see also Fig. XXVI. 2, 3). *Homocrinus*, Hall (1852, em. Bather, 1893), Silurian and Devonian, N. America and Europe; RA rhomboid and smaller. *Thenarocrinus*, Bather (1890), Silurian, England; large sac, anal area widened by RA sinking between BB. **Family 2. Botryocrinidae.** Dendrocrinoidea with arms bifurcating in two main rami with armlets or pinnules; RA usually small and quadrangular or absent. This family connects Dendrocrinidae with Decadocrinidae, and it is difficult to diagnose it so as to include all of the closely related forms. Genera—*Botryocrinus*, Angelin (1878, em. Bather, 1891; syn. *Sicyocrinus*, Ang.), Silurian and Devonian, Gotland, England, Canada; small RA, large anal sac, often coiled; arms range from irregularly dichotomous, through ramuliferous, to pinnulate (Fig. XCVII., see also Figs. III., XIII., and XXI.). *Gothocrinus*, Bather (1893), Silurian, Gotland, has a cup like *Dendrocrinus* with ramuliferous arms. *Mastigocrinus*, Bather (1892), Silurian, England, has very long, finely dichotomous arms, no RA (for anal sac, see Fig. XLVIII.). *Gastrocrinus* and *Rhadinocrinus*, Jaekel (1895), Devonian, Germany, are, respectively, like a *Botryocrinus* with cirri in whorls of 5 (Fig. XVII. 1), and a *Gothocrinus* with minute ramules. *Cosmocrinus*, Jaekel (1898), Devonian, Germany and N. America, has broad cup of *Botryocrinus* type, arms pinnulate, and with ramuli on the inner side of the two main rami. *Vasocrinus*, Lyon (1857, em. W. & Sp., 1879), Devonian to Carboniferous, N. America, scarcely differs from *Botryocrinus*. *Barycrinus*, Meek & Worthen (1868, em. W. & Sp., 1879), Carboniferous, N. America and England, has heavier cup-plates and large stem-lumen. *Goniocrinus*, Miller & Gurley (1890), Waverly Group, Iowa, has no RA, and has cirri like *Gastrocrinus*. *Atelestocrinus*, W. & Sp. (1886), Carboniferous, N. America, is distinguished by absence of an arm from ant. R; large RA supporting *rt* (Fig. XCVIII.); arms ramuliferous. *Streptocrinus*, W. & Sp. (1886; redescr. Bather, 1893; syn. *Ophiocrinus*, Ang. *non* Salter), has branched arms, coiling inwards, with pinnule-like processes arising irregularly from sides of Br; no RA, anal sac coiled. **Family 3. Lophocrinidae.** Dendrocrinoidea with only 1 ramus to each arm, with ramuli springing from the alternate sides of every second Br; with no RA, but *x* supporting on its shoulders 2 plates of a delicate anal sac. Genus—*Lophocrinus*, H. v. Meyer (1858; redescr. Jaekel, 1895; syn. ? *Carduocrinus*, v. Koenen), Upper Carboniferous, Germany.

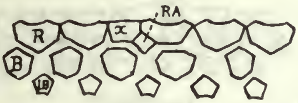


Fig. XCVII.
Analysis of cup in *Botryocrinus*.

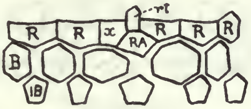
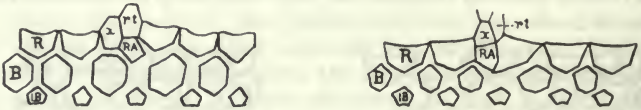


Fig. XCVIII.
Analysis of cup in *Atelestocrinus*.

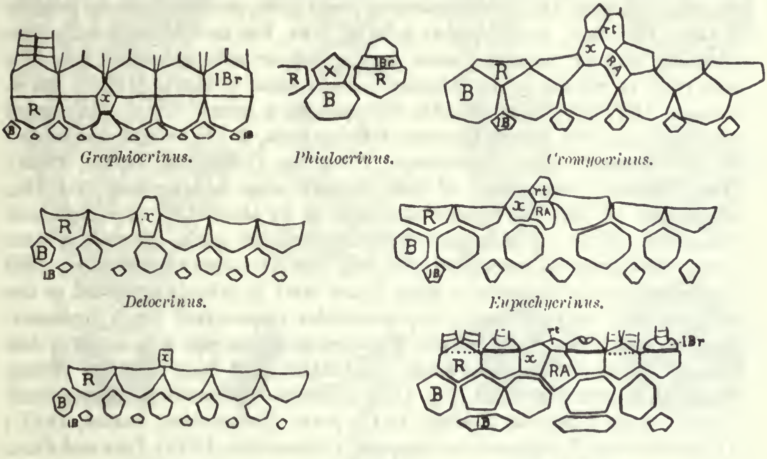
A similar evolution of arm-structure to that seen in Botryocrinidae produced a long series of genera with pinnulate arms, for the most part clearly forking into two rami, and rarely branching more than once again, but in some genera branching more often. All at first had an anal area more complicated than that of Dendrocrinus, in that a fresh plate (*rt*) was inserted between *x* and r. post. R so as to rest on RA, while a corresponding plate (*lt*) appeared on the left of *x*. Family 4. Scaphiocrinidae (= Poteriocrinidae, Auctt., greatly restricted). Dendrocrinoidea with dichotomous, usually much branched, pinnulate, stout arms, with facet occupying nearly full width of R ; with *x*, RA, *rt*, and *lt*, in anal area of cup, supporting a large plicated sac (Fig. XCIX.). Carboniferous of N. America and Europe, a few Devonian. Genera—*Scaphiocrinus*, Hall (1858, em. W. & Sp., 1886 ; synn. *Hydriocrinus*, Trautschold ; *Abrotocrinus*, Mill. & Gurl.), and *Poteriocrinus*, Miller (1821, em. W. & Sp., 1881), differ in little but the greater definiteness and less width of the facet in the latter; each has a long anal sac (Fig. XXVI. 4). *Woodocrinus*, de Koninck (1854 ; synn. *Philocrinus*, de Kon. ; *Pachylocrinus*, W. & Sp.), has shorter cup, arms, and sac. In *Aulocrinus*, W. & Sp. (1897), the sac forks. *Zeacrinus*, Hall (1858, em. W. & Sp., 1886), has a short, stout sac, around which the wide arms fit closely. *Coeliocrinus*, White (1863), and *Hydreionocrinus*, de Kon. (1858), differ from *Zeacrinus* in having the sac respectively balloon-shaped and mushroom-shaped. *Bursacrinus*, Meek & Worthen (1861 ; syn. *Synyphocrinus*, Trautschold), has arms like *Zeacrinus*, but no anal except *x* in the cup ; it is in the latter respect the morphological equivalent of *Graphiocrinus* (*infra*). Family 5. Scytalecrinidae. Dendrocrinoidea with forked, pinnulate, slender arms ; anal structures as in *Scaphiocrinus*. Genera—*Scytalecrinus*, W. & Sp. (1879, syn. *Dactylocrinus*, Sladen *non* Quenst.), and *Decadocrinus*, W. & Sp. (1879), both Carboniferous, differ chiefly in shape of cup, conical in the former, saucer-shaped in the latter, which thus leads on to : Family 6. Graphiocrinidae. Dendrocrinoidea with forked pinnulate arms and saucer-shaped cup, concave at base, and containing *x*, but no RA (Fig. C.). In many points resemble the earlier Encrinidae, but have not such thick cup-plates or large muscle-fossae. Middle and Upper Carboniferous. Genera—*Graphiocrinus*, de Koninck (1853), *Aesiocrinus*, Miller & Gurley (1890), *Delocrinus*, Miller & Gurley (1890 ; syn. *Ceriocrinus*, White *non* Desor). In this and the succeeding families the biserial arrangement of Br first assumes prominence ; it had already appeared as an occasional gerontic character at the distal end of the rami, but now is found in all except their most proximal portions, accompanied by shortening of the arm. Family 7. Cromyocrinidae. Dendrocrinoidea with simple or bifurcating, stout, pinnulate, usually



Poteriocrinus. Fig. XCIX. *Zeacrinus.*

Scaphiocrinidae. Analyses of cups.

biserial arms; with cup- bowl- or saucer-shaped, composed of stout plates, RR having muscle-fossae gradually more pronounced; with *x* always, and RA usually, present in cup, RA often supporting *rt* (Fig. C.). There is much confusion in the nomenclature of this and allied families, and the following names may not be used in what will ultimately prove the correct sense. Genera—*Cromyocrinus*, Trautschold (1867), and *Eupachycrinus*, Meek & Worthen (1855, em. W. & Sp., 1886), Middle and Upper Carboniferous, Europe and N. America, are closely allied; *x*, RA, and *rt* in anal area. *Agassizocrinus*, Shumard ex Troost MS. (1853; syn. *Astylocrinus*, C. F. Roemer), Kaskaskia group, N. America, is a *Cromyocrinus* that loses its stem in adult life, while IBB fuse to a solid mass (cf. *Edriocrinus*, p. 191). *Tribrachiocrinus*, M'Coy (1847, redescr. R. Etheridge, fil., 1892; syn. *Pentadia*, Dana, *pars*), Permo-Carboniferous, Australia, has l. and r.



Graphiocrinus. *Phialocrinus.* *Cromyocrinus.*

Delocrinus. *Eupachycrinus.*

Erisocrinus. Fig. C. *Tribrachiocrinus.*

Analyses of cups of Graphiocrinidae, Cromyocrinidae, and Encrinidae.

pairs of IBB fused; single arms borne by ant., r. post., and l. post. RR; whether the other RR bore arms is a moot point. *Phialocrinus*, Trautschold (1879, em. R. Etheridge, fil., 1892, *non* Eichwald; syn. *Pentadia*, Dana, *pars*), Permo-Carboniferous, Australia, Russia, India; differs from *Acsiocrinus* and *Ceriocrinus* in little but greater thickness of cup-plates, especially RR, and has, as they, only *x* in cup. *Ulocrinus*, Miller & Gurley (1890), Upper Carboniferous, N. America, has large RA, but very small *x*, which rises partly above level of RR (Fig. XXIX.). From these genera we pass almost insensibly to: Family 8. Encrinidae. Dendrocrinoidea with forked, pinnulate, biserial arms, saucer-shaped cup, with stout plates and well-developed muscle-fossae; with no anals in cup, and with sac diminished or absent (Fig. C.). Genera—*Stemmatocrinus*, Trautschold (1867), Upper Carboniferous Limestone, Russia, has IBB fused into one. *Erisocrinus*, Meek and Worthen (1865), Lower to Upper Carboniferous, N. America, has 5 small IBB covered by the stem, and *x* rests on upper surface of adjacent r. and l. post. RR. *Encrinus*, C. F. Schulze

(1760, synn. *Chelocrinus* and [?] *Calathocrinus*, v. Meyer, *Flabellocrinus*, Klipstein, [?] *Cassianocrinus*, Laube, [?] *Traumatocrinus*, Wöhrmann, which = *Porocrinus*, Dittmar *non* Bill.), Trias, Europe, has 5 minute IBB, a lofty plated tegmen, small tube, but no distinct anal plate.

Another line of evolution, probably continuing that of the Graphiocrinidae, introduces the Articulate Grade of Dendrocrinoidea, of which the most important family and the first to appear is the FAMILY 9. PENTACRINIDAE. Dendrocrinoidea with pinnulate, uniserial arms, forking once or dichotomising many times, either regularly, or irregularly so that the minor branches become pinnulate ramuli; with a small, usually depressed patina, in which IBB are often minute or atrophied in adult (pseudomonocyclic, or, as Bigot has recently expressed it, "cryptodicyclic"); but the flexible tegmen extends some way up the arms, so that the proximal IBr, and sometimes some IIBr, are incorporated loosely in the dorsal cup; a slight anal tube or cone, but no distinct anal plates in either cup or tegmen; stem pentagonal or sub-pentagonal, usually with cirri in whorls of 5. Genera—*Dadocrinus*, v. Meyer (1847; see v. Koenen, 1887-95), Trias, Middle Europe, has a round or sub-pentagonal stem without cirri, pinnulate arms forking once, 2 IBr, which are united by several small iBr. *Holocrinus*, W. & Sp. (1886, em. Jaekel, 1893), Trias, Germany, has whorls of cirri, slender arms forking once, 3-4 IBr, not united by iBr, but tegmen stretches up to about IBr, cup high and constricted above. The family characters become more definite in later forms, which may be associated as a SUB-FAMILY—PENTACRININAE; IBB always minute or atrophied; stem bears cirri in whorls attached to the epizygal of a syzygial pair; its internodes transversed by 5 ligament-bundles, which are interradially disposed and give rise to a more or less petaloid figure on the joint-faces; root-attachment may exist in young, but is relinquished in adult (Fig. CI.). Genera—*Pentacrinus*, Blumenbach (1804; synn. *Polycerus*, Fischer, 1811, *pars; Extracrinus*, Austin, 1847; [?] *Chladocrinus*, L. Agassiz; see especially Quenstedt, 1875), Lias and Jura, Europe. Petaloid sectors of stem linear with delicately crenulate edges; cirri elliptical or compressed in section, in close-set whorls; IBB present in adult; RR prolonged downwards over proximal columnals, the prolongations being jointed; each arm has at least 4 rami with large pinnulate ramules on one side only. *Isocrinus*, v. Meyer (1837; synn. *Isis*, Linnaeus, *pars; Cainocrinus*, Forbes; *Picteticrinus*, de Loriol; *Cenocrinus* and *Neocrinus*, Wyv. Thomson; and *Pentacrinus*, sensu P. H. Carpenter[1]), Trias to Recent, now chiefly Caribbean and Pacific. Sectors of stem distinctly petaloid, with coarsely crenulate edges; cirri circular in section, the whorls further apart (Figs. XVI. 4, 5; XVII. 2, 3); IBB are visible in various Jurassic species, but become obsolete in later times (cf. Fig. XI.); BB may form a complete circlet (on which feature *Cainocrinus* was based), or may be minute and separated by RR; IBr 2, non-pinnulate; arms isotomous or nearly so; sacculi occur sparingly. See Guettard (1761), J. Müller (1843), P. H. Carpenter (1884), and Fig. XXIII. 3, 5, on p. 117. *Balanocrinus*, Agass. in Desor (1845; em. de Lor. 1879), Trias to Eocene.

---

[1] Carpenter chose to ignore all writers on Crinoidea before J. S. Miller. For the history of these names, see *Natural Science*, April 1898.

has columnals of circular or basaltiform section, with crenellations round the edge only, not along the sides of the sectors. *Austinocrinus*, de Loriol (1889), Cretaceous; columnals have a joint-surface like that of *Isocrinus*, but with finer striae radiating from the petals to the circular periphery. *Metacrinus*, P. H. Carp. (1884), W. Pacific, differs from *Isocrinus* in having 5-8 IBr, of which IBr$_{2 \text{ and } 3}$ always, and IBr$_{5 \text{ and } 6}$ usually, are united by syzygy, while each, except IBr$_1$ and the hypozygals, bears a pinnule; BB form a complete circlet. The members of this sub-family live in colonies, but can move about and anchor by the cirri at the distal end of the stem.

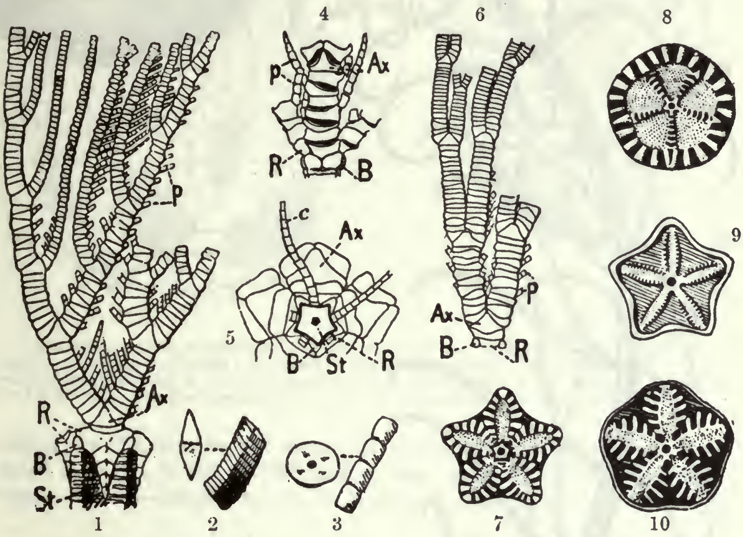


Fig. CI.

Pentacrininae. 1, *Pentacrinus fossilis*, portion of stem, patina, and portion of arm, showing rami, ramuli, and pinnules (*p*). 2, the same; portion of a cirrus and articular facet of a cirral. 3, the corresponding parts of *Isocrinus asteria*. 4, *Metacrinus Moseleyi*, cup and proximal portion of an arm. 5, *Isocrinus pendulus*, cup seen from below, with portion of stem, bearing cirri, still attached to it, and with proximal brachials. 6, a radius of the same, showing isotomy of arm. 7, *Isocrinus amblyscalaris*, joint-surface of an internodal columnal. 8, the same of *Balanocrinus subteres*. 9, the same of *Pentacrinus fossilis*. 10, the same of *Isocrinus asteria*. (From Bather, after P. H. Carpenter, de Loriol, von Meyer, and original.) 2, 3, 7, 8, 9, and 10 are slightly enlarged.

The stem is least specialised in *Balanocrinus*, most in *Pentacrinus*, in which it attained a length of 18 feet (Quenstedt thought 70). Family 10. Uintacrinidae. Dendrocrinoidea in which the arms fork once on IBr$_2$, are long and pinnulate, with numerous syzygies, and are incorporated in their proximal regions, together with proximal pinnules, in the dorsal cup, by means of iBr, iIIBr, and interpinnulars; there is no stem, but a centrale. Genus—*Uintacrinus*, Grinnell (1876), Upper Cretaceous, N. America, Germany, and England (Fig. CIII.), has a relatively large flexible theca and long arms. It was free-swimming and possibly pelagic. IBB usually obsolete. For detailed account, see Bather (1896). Family 11. Marsupitidae. Dendrocrinoidea (?) with pinnulate

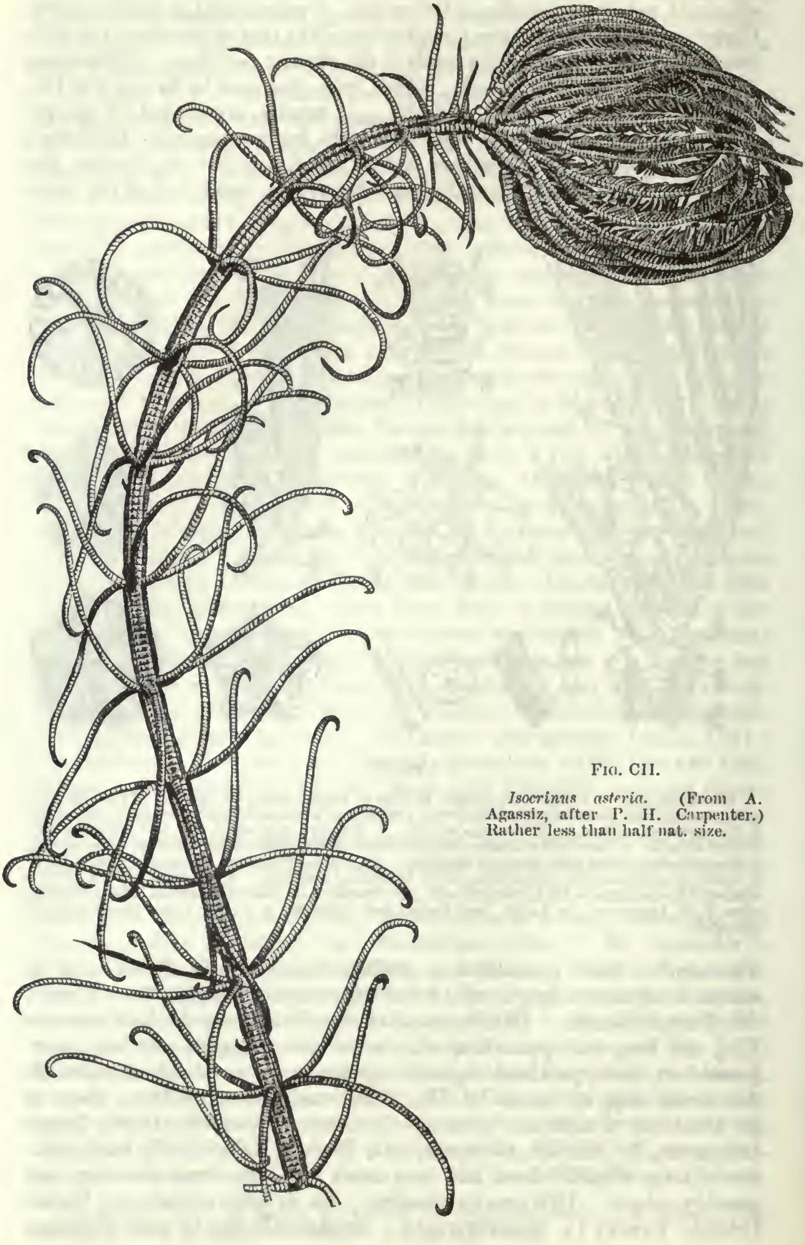
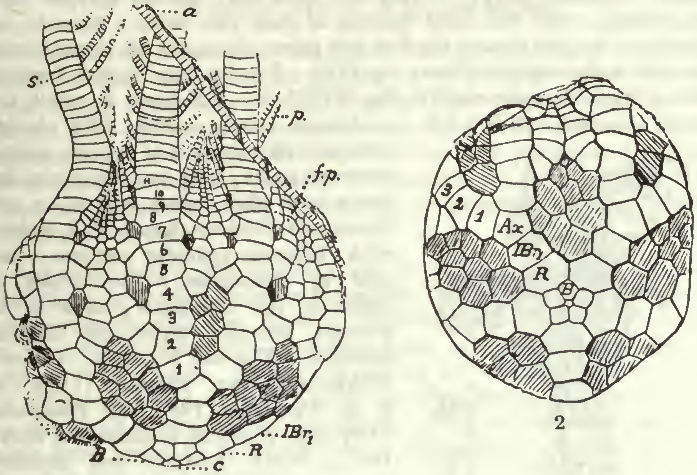


Fig. CII.

Isocrinus asteria. (From A. Agassiz, after P. H. Carpenter.) Rather less than half nat. size.

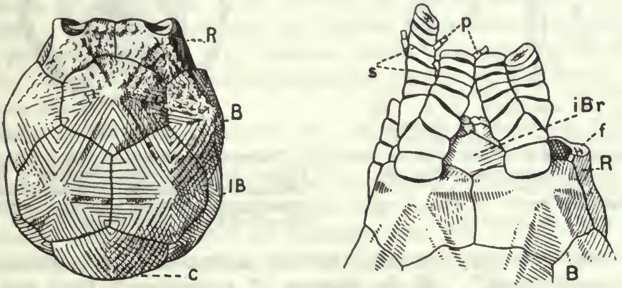
arms, short in proportion to cup, borne on a sharply defined radial facet, and forking on IBr_2 (further branching unknown); they are loosely



1 Fig. CIII. 2

Uintacrinus socialis, Upper Cretaceous of America, $\frac{2}{3}$ nat. size. 1, from the side. 2, from below. *c*, centrale; *B*, basals; *R*, radials; IBr_1, first primibrach; *Ax*, primaxil; 1, 2, 3, etc., secundibrachs, bearing *p*, pinnules, some of which are included in the walls of the cup, viz. *f.p.*; *s*, syzygy. The intercalated plates, which bind these elements together, are shaded.

united by iBr, but do not merge in the dorsal cup. Cup large, composed of 5 RR, 5 BB, 5 IBB, and a large centrale, with no trace of a stem. Genus—*Marsupites*, J. S. Miller ex Mantell MS. (1821; synn.



1 Fig. CIV. 2

Marsupites testudinarius. 1, the cup from the side, showing the character of the ornament; (from Brit. Mus. specimen, E2018), × $\frac{2}{3}$. 2, the radials and proximal region of the arms (from Brit. Mus. 5482), nat. size. *C*, centrale; *f*, fulcral ridge of radial facet; *p*, pinnules; *s*, syzygies. Other letters as usual.

Sitularia, Cumberland; *Marsupiocrinus*, de Blainville), Upper Cretaceous, England and Germany (Fig. CIV.; see also Fig. XVII. 4). The relations of the genus are not yet clear. Family 12. Bathycrinidae. Dendrocrinoidea (?) in which the arms fork once on IBr$_2$; IBr$_{1 \text{ and } 2}$ and all IIBr, except IIBr$_{3,\ 6,\ \text{and}\ 9}$, are united in pairs by trifascial articulation (*apud* Carpenter, see Fig. XXIII. 2), which may become syzygial (*apud* Danielssen); only the distal brachial of each pair bears a pinnule, and there are no pinnules on the first few pairs; the arms are loosely incorporated in the cup to half-way up IIBr$_3$; Iax has large muscle-fossae on strong wing-like processes (cf. Fig. XVIII. 6). BB fused in adult to a single discoidal ossicle; RR also become closely united; IBB obsolete. Interambulacral areas of tegmen contain scattered small plates, and sometimes each has a large plate, which may be an oral. Columnals dicebox-shaped and twisted, with bifascial articular surfaces; each said by Danielssen to be formed by fusion of two columnals; those in the younger, proximal region are thin and discoidal. The root branches. Genus—*Bathycrinus*, Wyv. Thomson (1872; see P. H. Carpenter, 1884, and Danielssen, 1892; syn. *Ilycrinus*, Danielssen & Koren, 1877), North Atlantic and Southern Ocean, at 750-1500 fathoms (Fig. CV.). Carpenter places this in the Bourgueticrinidae on the grounds of its resemblance to *Rhizocrinus*, while admitting that "the differences between the two genera are much greater than their resemblances." If the absence of a proximale have the value claimed for it by Wachsmuth & Springer, the two genera must go into different orders. The interradial axial nerve-cords correlated with the BB fork first within the sutures between RR, and, in Carpenter's opinion, the basi-radial strands take the place of a ring-commissure; but Danielssen describes a ring-commissure (see Fig. CVI.). There are 3 water-pores in each IR. The crown separates very easily from the BB and stem, and may be replaced by a fresh crown (Fig. CV. 2). Sacculi occur. (See also Fig. LIII.)

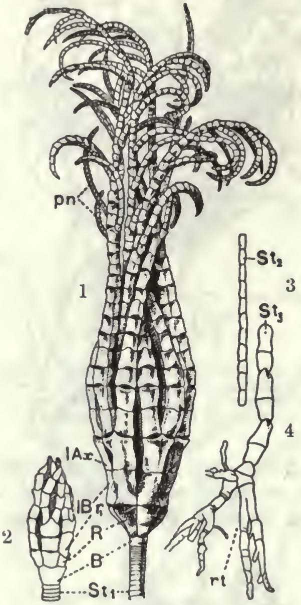


FIG. CV.

Bathycrinus. 1, crown of *B. Aldrichianus*, nat. size (after P. H. Carpenter). 2, 3, and 4, *B. Carpenteri* (after Danielssen). 2, new radials and arms on an old base and stem, × 4 diam. 3 and 4, stem fragments, nat. size. *pn*, pinnules; *rt*, root-cirri; *St*$_1$, proximal region of stem; *St*$_2$, median ditto; *St*$_3$, distal ditto.

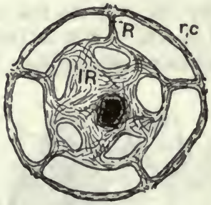


FIG. CVI.

Transverse section of the dorsal nervous system in *Bathycrinus Carpenteri*, diagrammatised from Danielssen. *IR*, interradial cords which pass up between radials; *R*, radial cords, connected by *rc*, the ring-commissure.

ORDER 2. **Flexibilia**, Zittel

(= ARTICULATA, W. & Sp. *non* Müller).

Dicyclica in which proximal Br are incorporated in the dorsal cup, either by their own sides, or by iBr, or by a finely plated skin, but never rigidly; plates may occur between RR. Tegmen flexible, with distinct Amb and numerous small iAmb; mouth and food-grooves remain supra-tegminal and open. The top columnal is a persistent proximale, often fusing with IBB, which are frequently atrophied in the adult. Arms non-pinnulate (Grade Impinnata), or pinnulate (Grade Pinnata), but always uniserial.

As in the case of the Distincta and Articulata among the Dicyclica Inadunata, so the line between the grades Pinnata and Impinnata corresponds roughly with that between Palaeozoic and Mesozoic time. But in the present order the grades are more self-contained and the gap between them greater. In fact, we are by no means certain that they are rightly described as mere grades; in other words, that the Pinnata are the lineal descendants of Impinnata. The two divisions may have arisen from Inadunata independently, springing from pinnulate and non-pinnulate forms respectively.

GRADE 1. **Impinnata.**

Flexibilia, in which all plates of the crown are united by loose suture or muscular articulation. IBB 3, the primitive r. post. remaining as the small unfused IB. Br usually united by waving sutures, the lower edge of each frequently with a projection that fits into a depression on the plate below, and often becomes a separate patelloid plate. Arms isotomous, or rami may bear ramules on one or both sides, but no pinnules. Ventral groove wide and shallow; axial canal separated from it in proximal region. 5 O, between which food-grooves pass to the mouth. Stem round; proximal columnals very short, and usually wider than the others.

Many of the earlier genera can be distinguished from Dicyclica Inadunata only by the greater thickness and more elaborate sutural union of their plates, and the greater width and less length of the arms. It is the combination of massiveness with flexibility that characterises the Grade. There is never an elaborate anal sac. Within the Grade Impinnata can be traced the evolution of heterotomous arm-branching of two types, also an increase in number of iBr. The genera seem to merge into one another, and are as yet too ill-defined to be grouped into families on a sure genetic basis. The following arrangement represents similarities of structure rather than lines of descent.

FAMILY 1. ICHTHYOCRINIDAE. Impinnata with no iBr, with isotomous arms, closely abutting by their sides. Genera—*Pycnosaccus*, Angelin (1878; syn. *Oncocrinus*, Bather), Silurian, Gotland, England, and N. America, has a cup like that of *Barycrinus*, with *x* and RA, and with strong axial folds (Fig. CVII.); arms, though abutting above, are distinct below and do not interlock ; columnals solid, moniliform, alternating in thickness. *Lecanocrinus*, Hall (1852), Silurian and Devonian, N. America and Europe, differs only in greater smoothness of cup and approximation of arms, which may even interlock by the alternating edges of the Br. *Cyrtidocrinus*, Angelin (1878), only known from cup, which appears to be like that of *Lecanocrinus*, but is said to have 4 BB. *Clidochirus*, Ang. (1878), Silurian, Gotland ; arms abut, but do not interlock ; no RA, but 3 anals in vertical series rest on truncate post. B. *Mespilocrinus*, de Koninck (1853), Lower Carboniferous, Belgium, England, and N. America, differs from last-mentioned in having each arm curved over to the right, so that they all fold with a sinistral twist (as seen from above) ; IBr$_1$ wedge-shaped, broader on left. *Nipterocrinus*, Wachsmuth in Meek & Worthen (1868), Carboniferous, N. America, should perhaps come here. *Ichthyocrinus*, Conrad (1842), Silurian, N. America and Europe, has no anals ; arms abut all round and interlock by edges of Br (Fig. CVIII.). Family 2. Gazacrinidae. Impinnata (?) with a single large iBr in each interradius, the posterior (anal) resting on truncate edge of large post. B ; arms isotomous ; tegmen of 5 O of Cyathocrinoid type, surrounding a peristome which is covered by fused proximal Amb, and supporting Amb along their edges ; food-grooves fork on the tegmen (Fig. CIX.). Genus—*Gazacrinus*, S. A. Miller (1892 ; syn. *Idiocrinus*, W. & Sp.), Silurian, N. America, is referred to the Camerate Family Dimerocrinidae by W. & Sp. (1897). Its dorsal cup does not differ essentially from that of *Anisocrinus* (*infra*), but the number of IBB is uncertain. The tegmen, scarcely of either Flexible or Camerate type, suggests recent descent from Inadunata. Family 3. Taxocrinidae. Impinnata with iBr, which usually

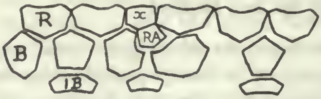


Fig. CVII.
Analysis of cup in *Pycnosaccus*. (After Bather.)

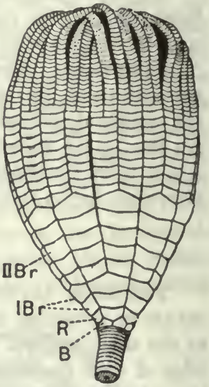


Fig. CVIII.
Ichthyocrinus piriformis, slightly restored from Brit. Mus. 40214. (Nat. size.)

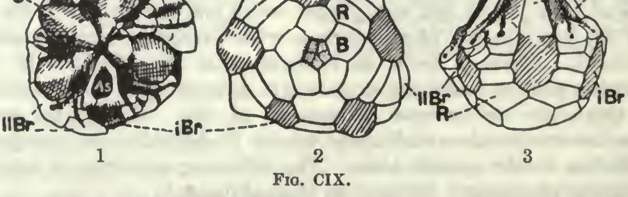


Fig. CIX.
Gazacrinus. (Diagrammatised from Wachsmuth & Springer), × 2 diam. 1, *G. inornatus*, tegmen with almost all ambulacrals removed. 2, *G. ventricosus*, dorsal view. 3, same, side view, with proximal ambulacrals (*P*) in position. *As*, passage for rectum through posterior oral ; *v.g*, ventral grooves passing between edges of orals. Other letters as usual.

are few and have the proximal larger than the rest; with isotomous arms which may abut but do not interlock; anals form a well-defined vertical series. Genera—*Gnorimocrinus*, W. & Sp. (1879, em. Bather, 1899), Silurian, Gotland; arms distinct, with 0-4 small iBr, and sometimes a few iIIBr; post. B reaches up to top of patina, between it and r. post. R is a RA, supporting the greater part of *x*, which bears a vertical series of 1 or 2 rows. *Anisocrinus* Angelin (1878), Silurian, Gotland, has abutting but not interlocking arms, a very large proximal iBr, with small triangular piece above; *x* differs from iBr only in resting on truncate edge of large post. B; no RA. *Taxocrinus*, Phillips in Morris (1843; synn. *Isocrinus*, Phill. *non* v. Meyer; *Cladocrinus*, Austin *non* Agass.; *Euryalecrinus*, Aust.; *Forbesiocrinus*, de Kon. *non* W. & Sp.), Silurian to Carboniferous, Europe and N. America, has arms more distinct, with few or no iBr, and occasional small iIIBr and iIIIBr; anals form a vertical series resting on truncated post. B, and seem to have supported a small free tube (Figs. CX. 1, and XXXVII.). *Homalocrinus*, Ang. (1878), Silurian, Gotland, has very small BB, abutting arms, large proximal iBr, followed by 1 or 2 in vertical series, occasionally 2 iIIBr, anals as iBr but resting on post. B; except for the isotomy of its arms, this genus closely resembles *Calpiocrinus*. FAMILY 4. DACTYLOCRINIDAE. Impinnata with iBr either few or numerous; with heterotomous arms, the rami bearing ramules; with anals in vertical series. Genera—*Calpiocrinus*, Ang. (1878), Silurian, Gotland and England, has minute often obsolete IBB, but fairly large BB; iBr few and variable, iIIBr occasionally present; anals 3-5, *x* resting on the small post. B; the IIBr rami bear unbranched ramules on their inner sides, the proximal ramule much larger than the rest (Fig. CX. 3). *Lithocrinus*, W. & Sp. (1879, emend. Bather, 1899; syn. *Forbesiocrinus*, Ang. *non*. de Kon.), Silurian, Gotland, differs from *Calpiocrinus* in larger size of BB, greater number of iBr, branching of ramules; the latter characters make the arms less apposed to one another (Fig. CX. 2). *Dactylocrinus*, Quenstedt

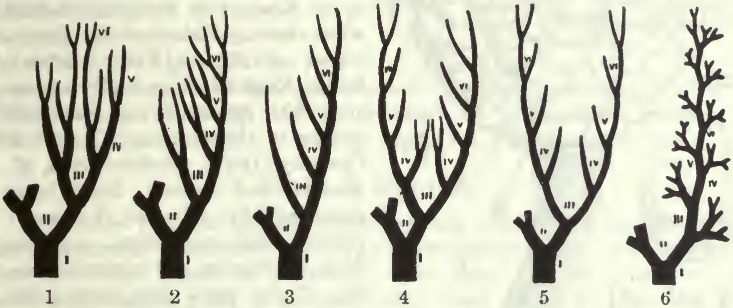
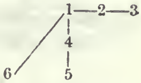


FIG. CX.

Diagrams of the arm-branching in Taxocrinidae and Dactylocrinidae. 1, *Taxocrinus tuberculatus*; 2, *Lithocrinus*; 3, *Calpiocrinus*; 4, *Dactylocrinus*; 5, *Synerocrinus*; 6, *Onychocrinus exsculptus*. These do not form a continuous evolutionary series, but their relationship may be indicated thus—



(1876, based on *Dimerocrinus oligoptilus*, Pacht; probably includes *Aristocrinus* or *Callawaycrinus*, Rowley, 1895), Silurian (?) and Devonian, N.-W. Europe and N. America; iBr few, proximal large; *x* rests on large truncate post. B, a little to the right, and supports numerous smaller plates in somewhat irregular vertical series; the IIIBr rami bear ramules on the sides towards the middle of the dichotom, the proximal ramule branches again (Fig. CX. 4). *Synerocrinus*, Jaekel (1897), Carboniferous, Europe, has arms like *Dactylocrinus*, except that no ramules branch; it also differs in having 3-8 iBr, perhaps more, with occasional iIIBr and iIIIBr; *x* rests on post. B (Figs. CX. 5, and CXI.). This genus probably includes the Belgian species erroneously referred by de Koninck to *Taxocrinus nobilis* when erecting *Forbesiocrinus*. *Euryocrinus*, Phillips (1836), Carboniferous, England, is probably a close ally, but its arms are not well known. *Onychocrinus*, Lyon & Casseday (1859), Carboniferous, N. America and Ireland, has a large proximal iBr followed by small plates, often numerous, merging with the tegmen and ventral covering of the arms, but leaving the arms more free than usual in the sub-order; IIBr rami bear branching ramules, either along each side or in clusters at end, but the heterotomy is always bilateral, not unilateral as in all the genera just mentioned—a fact suggesting that *Onychocrinus* should form a distinct family or, at least, sub-family (Fig. CX. 6); anals 3-5 resting on post. B (see also Fig. XVII. 4). FAMILY 5. SAGENOCRINIDAE. Impinnata with over 20 iBr, 6 or more iIIBr, and variable number of iIIIBr; arms isotomous or almost so, to VIBr or beyond; anals not a distinct series, but represented by greater width or number of iBr in post. IR. Genera—*Sagenocrinus*, Austin (1843), Silurian, Europe and N. America, has RA sunk between post. and r. post. BB, so that proximal iBr is supported between post. B and RA (Fig. XXIV*a*). In "*Forbesiocrinus Agassizi*," Carboniferous, N. America, which may be placed in this family, post. B supports 2 iBr, and there are considerably more iBr in this IR. Patelloid plates are richly

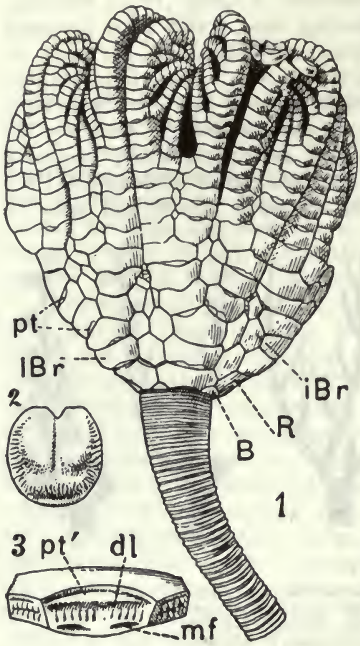


FIG. CXI.

Synerocrinus incurvus, from Brit. Mus. E6707. 1, from the right anterior side, × ¾. 2, joint-surface of a brachial, × 3 diam. 3, a radial, showing articular surface for first primibrach, and on either side the surfaces of loose suture with interbrachials, × $\frac{3}{2}$. *B*, basals, which pass under the cup, the larger posterior basal is just visible on the left; *dl*, fossa for dorsal ligament; *mf*, muscle-fossa; *pt′*, surface for attachment of patelloid plate (*pt*). Other letters as usual.

developed, but are absent from *Sagenocrinus.* Otherwise the two genera agree closely.

The following genera are placed provisionally in the Impinnata :—*Edriocrinus*, Hall (1859), Devonian, N. America (Fig. CXII.), when young is attached by BB, but is free-floating in adult ; BB become fused into a bowl-shaped mass, supporting 5 RR and *x* ; arms broad, with low Br, isotomous. *Cleiocrinus*, E. Billings (1856 ; see W. & Sp., 1886), Ordovician, Canada ; IBB and BB hidden by stem ; RR small and separated by a large pentagonal interradial ; arms isotomous to about VIIBr, and all appear to interlock and to be joined by close suture ; post. IR supports a vertical series of anals, which reach the full length of the arms. *Rhopalocrinus*, W. & Sp. (1879), is based on "*Taxocrinus gracilis*," Schultze, Devonian, Eifel ; it perhaps belongs to Dicyclica Inadunata.

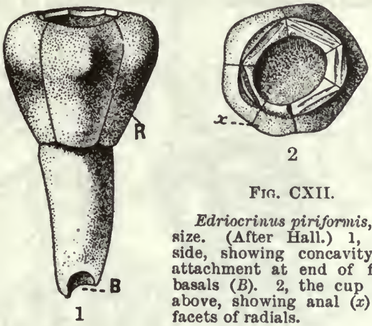


FIG. CXII.

Edriocrinus piriformis, nat. size. (After Hall.) 1, from side, showing concavity for attachment at end of fused basals (*B*). 2, the cup from above, showing anal (*x*) and facets of radials.

GRADE 2. **Pinnata.**

Flexibilia with BB and RR united by close suture, RR and proximal Br by muscular articulation or syzygy ; pseudomonocyclic ; arms pinnulate and either simple or isotomous ; axial canal separate from ventral groove throughout ; Iax is generally IBr_2, rarely IBr_1 ; 5 O present in early stages and sometimes in adult, but usually atrophy ; anals do not form part of the dorsal cup in the adult. Stem round, pentagonal, or elliptical in section, proximal columnals often forming a widened cone.

This group is confined to Mesozoic and later times, and there is no evidence that it is descended from the Palaeozoic Impinnata ; it may be an offshoot from Triassic Dicyclica Inadunata, from which it is distinguished by the mode of growth of the proximal columnals.

FAMILY 1. APIOCRINIDAE. Pinnata in which the patina consists of 5 BB and 5 RR ; arms incorporated to a very variable extent in the cup, and iBr may be present ; columnals round or pentagonal in section, their joint-surfaces marked with radiating striae, and sometimes tubercles in the middle ; no cirri ; root, when present, encrusting. (For fossil forms, see de Loriol, 1883.) Genera—*Millericrinus*, d'Orb. (1840 ; synn. *Ceriocrinus* and *Pomatocrinus*, Desor ex König), Trias (?) to Lower Cretaceous, Europe ; IBr_1 united to R by muscular articulation, and to Iax by close suture ; arms isotomous, free from IBr, or proximal Br united by tegmen, or a few small iBr developed ; except for the proximale, the upper columnals are rarely widened (Fig. XVII. 7). In some species (Fig. LII.) the crown breaks off from the root, the stem is gradually resorbed, and a free-floating stage attained. *Apiocrinus*, Miller (1821), Jurassic, Europe ; IBr_1 united to R probably by ligament, not by muscular articulation, and to Iax by incomplete syzygy ; $IIBr_1$ united to Iax by articulation ; arms isotomous, incorporated in cup at least up to $IIBr_3$; iBr few and irregular ; the upper columnals widen gradually, and, with the proximale, form a cone passing into the cup (Fig. XVII. 5, 6). *Guettardicrinus*, d'Orbigny (1840), Upper Jurassic, differs from *Apiocrinus* only in the union of $IIBr_1$ to Iax by close suture, the incorporation of a greater number of IIBr in the cup, and the presence of more iBr ; it is the acme of this line of development. *Acrochordocrinus*, Trautschold (1859 ; synn. *Cyclocrinus*, d'Orb. *non* Eichw. ; *Mespilocrinus*, Quenst. *non* de Kon.), Jurassic and Lower Cretaceous ; columnals only. *Calamocrinus*, A. Agassiz (1890,-92), 392-782 fathoms, Galapagos Is. and B. of Panama (Fig. CXIII.). Patina distinct, owing to restriction of facet to $\frac{2}{3}$ width of R ; BB tend to be fused ; RR laterally united by ligament ; r. and l. post. RR slightly longer than the others. IBr_1 united to R by

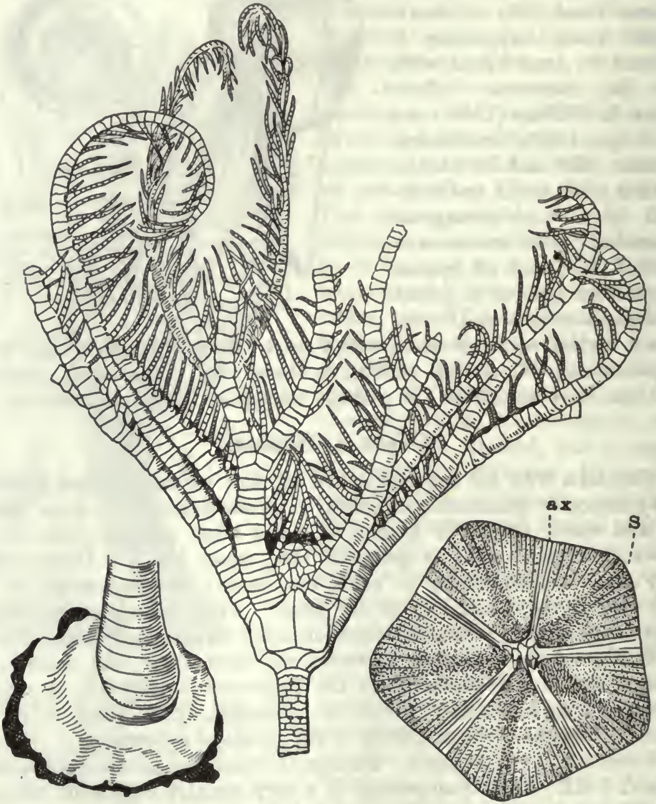


Fig. CXIII.

Calamocrinus Diomedae. 1, the crown and proximal portion of the stem from the right posterior interradius, × $\frac{2}{3}$. 2, the root, nat. size. 3, the interior of the basal circlet, from above, showing the anchylosed sutures (*S*) and the axial cords (*ax*) radiating from the central chambered organ, × $\frac{5}{1}$. (After Agassiz.)

muscular articulation, and to IBr_2 by incomplete syzygy. Arms heterotomous; each gives off 5 unbranching rami nearly as stout as the main stem, 2 to right and 3 to left, or *vice versa;* the first main-axil is the 10th or 11th brachial, succeeding branches are at much greater intervals; pinnules occur below IAx, on $IBr_{4, 6, 8,}$ or $IBr_{4, 6, 7, 9,}$ those being as a rule epizygals. There are distinct Amb and adAmb, both in arms and tegmen. The proximal region of the arms is fixed by the tegmen, so that the grooves of the proximal pinnules rise from the tegminal food-groove (Fig. XXIV.). Small iBr rest on shoulders of RR and merge into imperforate iAmb, and these pass into poriferous iAmb; 5 imperforate plates at the interradial angles of the peristome are taken by Agassiz for O (Fig. CXIV.). Stem long, smooth; root encrusting (Fig. CXIII. 2). **Family 2. Bourgueticrinidae.** Pinnata in which the patina consists of 5 BB

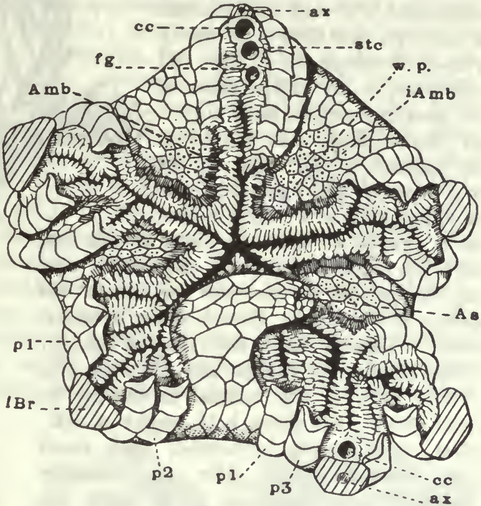


Fig. CXIV.

Tegmen of *Calamocrinus Diomedae*, with the arms and pinnules cut off down to the level at which they become fixed in the calyx. *Amb*, ambulacrals or covering-plates; *As*, anus; *ax*, axial canal of arm; *cc*, coeliac canal of arm; *fg*, food-groove of anterior arm where it joins the tegminal food-groove; *IBr*, primibrach; *iAmb*, interambulacrals, both perforate and imperforate; *p1*, first or proximal pinnule; *p2*, second; *p3*, third pinnule; *stc*, subtentacular canal of anterior arm; *w.p*, water-pores. (After Agassiz), × $2\frac{2}{3}$.

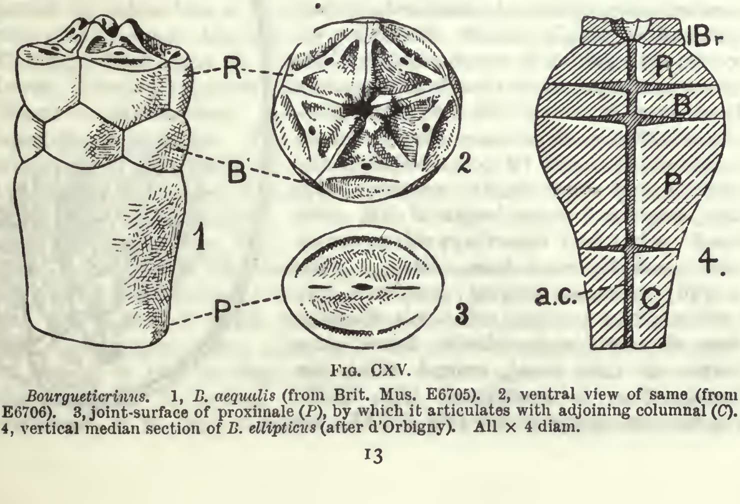


Fig. CXV.

Bourgueticrinus. 1, *B. aequalis* (from Brit. Mus. E6705). 2, ventral view of same (from E6706). 3, joint-surface of proximale (*P*), by which it articulates with adjoining columnal (*C*). 4, vertical median section of *B. ellipticus* (after d'Orbigny). All × 4 diam.

forming a closed ring and 5 RR with high muscle-plates; arms incorporated to a very slight extent in the cup; and then only loosely without development of iBr; all columnals, or all except those in the proximal region, have elliptical joint-surfaces with a grooved and toothed fulcral ridge in the long diameter and ligament-fossae on either side of it; each columnal is twisted so that the ridge at one end lies at an angle to that at the other end; cirri may be present at the root end or in the middle of the stem. Sacculi occur in recent forms. Genera—*Bourgueticrinus*, d'Orbigny (1840), Cretaceous, Europe and Alabama (Fig. CXV.); sides of cup vertical or sloping inwards above; BB about half height of RR; radial facet small, horizontal, with small dorsal ligament-fossa; IBr$_{1\ \text{and}\ 2}$ laterally connected with adjoining rays, arms unknown; proximale enlarged, circular; columnals of proximal region circular, widening upwards; those of middle and distal regions twisted, elliptical; fulcral ridge continuous around axial canal, ligament-fossa broad and shallow; cirri rare except at root. *Mesocrinus*, P. H. Carpenter (1881), Cretaceous, Sweden, Germany; sides of cup slope outwards; BB short; radial facet large, slopes upwards to centre, with larger ligament-fossa; arms unknown; proximale small and circular; proximal columnals circular, narrowing upwards; the rest as in *Bourgueticrinus*, but ligament-fossa deeper; cirri sometimes numerous. *Rhizocrinus*, M. Sars (1864,-68; synn. *Conocrinus*, d'Orb.; *Democrinus*, Perr.), Eocene to Recent; Atlantic, 73 to (?) 1900 fathoms: sides of cup slope slightly outwards; BB high, may be 7 times height of RR, often fused; radial facet slopes upwards to centre, with small ligament-fossa; IBr$_{1\ \text{and}\ 2}$ free laterally, arms not forking; proximale thin and discoidal; proximal columnals discoidal, those of middle region slender, fulcral ridge broken at axial canal, around which the ligament-fossa is concentrated (Fig. XLIX. 7); no cirri except at root (Fig. CXVI.; see

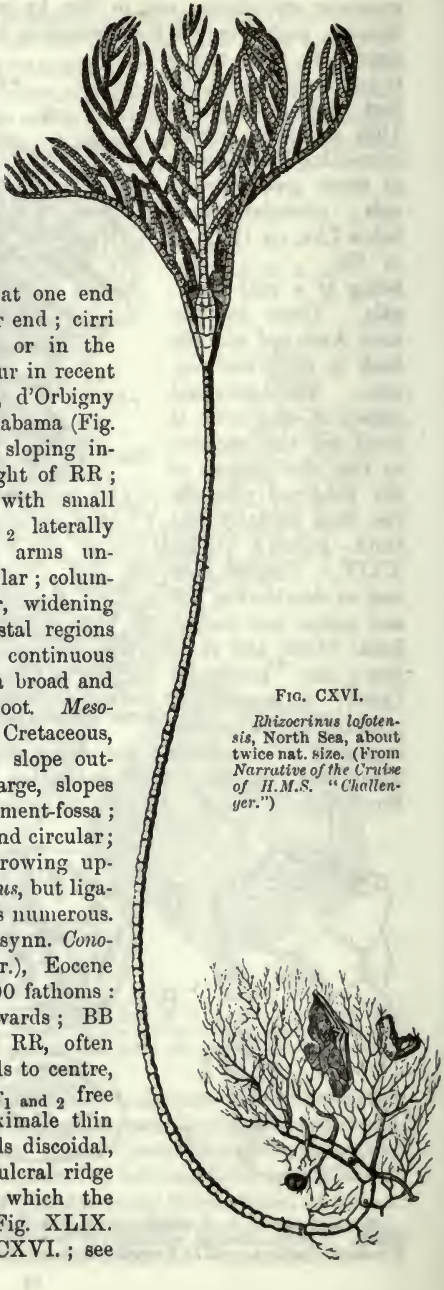


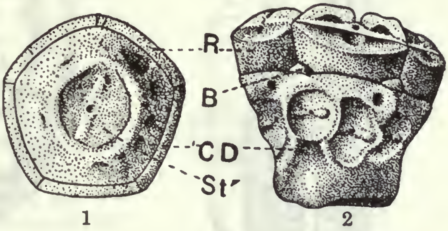
FIG. CXVI.

Rhizocrinus lofotensis, North Sea, about twice nat. size. (From *Narrative of the Cruise of H.M.S. "Challenger."*)

also X., XXIII. 4). Family 3. Antedonidae. Pinnata in which the patina consists of 5 small BB, not forming a closed circlet, and RR with large high muscle-plates and facet approaching horizontal; cavity enclosed by RR is minute; mouth endocyclic; proximal Br loosely incorporated in cup; columnals as in Bourgueticrinidae, but usually lost in the adult, except the proximale and adjoining columnals which fuse with one another and with IBB to form a single ossicle, the "centrodorsal," which bears cirri; root when present, encrusting. O and *x* present in brephic stage, but not in adult. Sacculi almost always present. (See structural details of *Antedon*, Figs. IX., XV., XVIII. 2, 3, 4, XIX., XXX., XXXIII., XLVI., XLVII., XLIX. 8, 9, LIV., LV.) Genera—*Thiollierícrinus*, Étallon (1859), Jurassic and Cretaceous of Switzerland, France, and Portugal (Fig. CXVII.); scarcely differs from *Mesocrinus*, except in the reduction of BB and presence of a cirriferous centrodorsal at the top of the fairly stout stem; our knowledge of this most important form is due to de Loriol. The remaining Antedonidae retain the portion of stem below the centrodorsal only in the brephic stage, while their BB further diminish during geological periods, their adcentral portions fusing into a small 10-rayed plate, the "rosette," which lies above the chambered organ, and in some species of *Antedon* is all that remains of BB. There is also traceable in the arms a gradual attenuation and, in many cases, increase of forking, with a partial or entire loss of calcified covering-plates. *Antedon*, de Fréminville (1811; synn. *Alecto*, Leach; *Comatula*, Lamarck, *pars; Hibernula*, Fleming; *Phytocrinus*, de Blainville; *Solanocrinus*, Goldfuss; *Hyponome*, Lovén; *Geocoma*, Fraas *non* d'Orb.; *et alia*), Lias to Recent, almost all seas, littoral to 2900 fathoms. Arms fork once or more; Amb usually present, especially on pinnules. The genus is divisible into 9 groups, differing in arm-structure and distribution. *Eudiocrinus*, P. H. Carp. (1882; syn. *Ophiocrinus*, Semper *non* Salter), Neocomian (?) to Recent, Pacific and B. of Biscay, 50 to 900 fathoms; differs from *Antedon* only in non-forking of arms. *Promachocrinus*, P. H. Carp. (1879), Pacific and South Sea, 70 to 1800 fathoms; 10 RR, probably a persistent meristic variation from more than one species of *Antedon*. Family 4. Atelecrinidae. Pinnata with patina of 5 BB forming closed circlet and no rosette, 5 RR with high muscle-plates; arms fork once, IIBr long, with no pinnules on first 8 or 16; no stem, but acorn-shaped centrodorsal, with cirri alternating in 5 vertical double rows; sacculi present. Genus—*Atelecrinus*, P. H. Carp. (1881), Cretaceous (?) to Recent, tropical Atlantic

Fig. CXVII.

Thiollierícrinus. 1, *T. flexuosus*, cup seen from below, no basals visible (from Brit. Mus. 49222*a*). 2, *T. Ribeiroi*, from the side, showing basals and facets for cirri (reconstructed from de Loriol's figures). *CD*, centrodorsal, still bearing facet (*St′*) for attachment to stem. × 2 diam.



and Pacific (Fig. CXVIII.). Family 5. Actinometridae. Pinnata with dorsal cup and centrodorsal on the Antedonid plan, but differing in the following points:—Mouth exocyclic and gut much coiled, with consequent larger cavity between RR, small muscle-plates, and facet approaching the vertical; further asymmetry shown in unequal and variable tegminal food-grooves, and in occasional ungrooved structure of some posterior rami, which may be shorter than the rest and without podia; no sacculi; no calcified Amb; proximal pinnules have a terminal serrated margin—"comb"; centrodorsal discoid, with cirri few, almost limited to its margin, and sometimes atrophied. Genus—*Actinometra*, Müller (1841, em. P. H. Carp., 1887; synn. [?] *Comaster*, L. Agassiz; *Comatula*, *pars; Phanogenia*, Lovén), Lower Jurassic to Recent, almost all seas, littoral to 800 fathoms. Divisible into 8 groups, differing in arm-structure and distribution. Family 6. Thaumatocrinidae. Pinnata with cup of 5 BB forming a closed ring, and 5 RR separated by 5 interradials resting on BB; Br not incorporated in cup; arms do not fork; 5 O, separated from cup-plates by relatively large iAmb; no Amb; no sacculi; anal tube in post. IR; post. interradial followed by 5 plates in vertical series forming a free appendage (Fig. CXIX.). Genus—*Thaumatocrinus*, P. H. Carp. (1883), a unique individual, probably young, South Sea, 1800 fathoms. Differs greatly from all other Pinnata; the structure of the cup is as in *Xenocrinus* (p. 165), the anal appendage is paralleled in some *Taxocrini* (cf. Fig. XXXVII.).

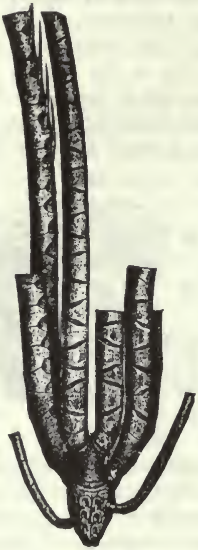


Fig. CXVIII.

Atelecrinus balanoides, with two cirri partly preserved and arms imperfect. (From A. Agassiz, after P. H. Carpenter.) × 2 diam.

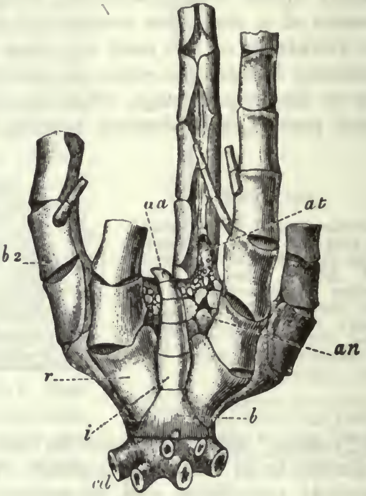


Fig. CXIX

Thaumatocrinus renovatus, from the anal side. *aa*, anal appendage; *an*, interambulacrals; *at*, anal tube; *b*, basal; b_2, second brachial; *cd*, centrodorsal; *i*, interradial; *r*, radial. (After P. H. Carpenter.) × $\frac{15}{4}$.

Family 7. Eugeniacrinidae. Pinnata with patina of 5 RR only, BB having been overgrown by RR and absorbed by a continuance of such a process as produced the rosette of *Antedon*. RR united by close suture, often fused. IBr_2 axillary, united to IBr_1 by syzygy or fusion. Rami 10, robust, incurving. Stem short; columnals cylindrical, high, with joint-surface granulate, or marginally striate; no cirri; root encrusting, lobed. All European (see de Loriol, 1883, and Jaekel, 1891). Genera—*Eugeniacrinus*, J. S. Miller (1821; syn. *Symphytocrinus*, König; *Caryophyllites*, Auctt. pre-Linn.), Bathonian to Lower Cretaceous (Fig. CXX.). Patina cylindrical or clove-shaped, with shallow depression for viscera; radial facets separated by processes; Iax rising above origin of IIBr into a 3-sided spine, which perhaps helped to support the tegmen; IIBr small. *Torynocrinus*, Seeley (1866; synn. *Cyrtocrinus*, Jaek.; ? *Hemicrinus*, d'Orb.), Upper Jurassic to Lower Cretaceous; patina and proximale fused, the ventral surface bent to one side and bearing stout arms. *Gammarocrinus*, Quenst. (1858; syn. *Sclerocrinus*, Jaek.), Upper Jurassic; patina massive, concave below. *Gymnocrinus*, de Lor. (1879, em. Jaek., 1891); Upper Jurassic; Iax remarkably developed. *Phyllocrinus*, d'Orb. (1849), Bajocian to Neocomian; RR have small facets and long spines. *Tormocrinus*, Jaek. (1891), Eocene, and *Trigonocrinus*, Bather (1889), Oxfordian, have very small radial facets, rounded spines, and a deep tubular cup-cavity; the latter differs in the loss and atrophy of certain rays. *Dolichocrinus*, de Loriol (1891; syn. *Tetanocrinus*, Jaek.), Upper Jurassic; RR form a tube 10 mm. long, 2·25 mm. wide, with interradial re-entrant angles at its base; the radial facets are of Bourgueticrine or Antedonid type, and if BB were present, as de Loriol supposes, the genus must be removed from this family. Family 8. Holopodidae. Pinnata with patina of 5 RR, usually fused, and enclosing a relatively wide cavity. BB presumably as in Eugeniacrinidae. O large, surrounded by a few iAmb. Iax fused to IBr_1 in adult, and supports stout, incurved, unbranching rami; no stem; attachment by base of patina. No sacculi. The arm-structure led Jaekel (1891) to combine these forms with the Eugeniacrinidae. Genera—*Holopus*, d'Orb. (1837), Tertiary of Italy, Recent, Caribbean Sea, shallow

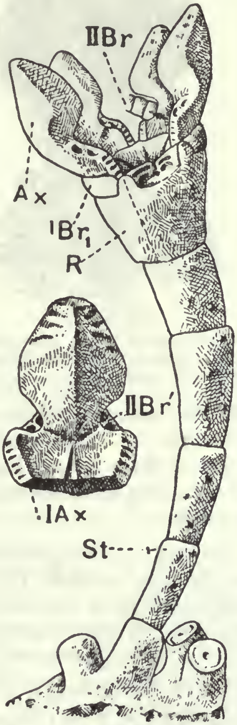


Fig. CXX.

Eugeniacrinus caryophyllatus, partial reconstruction (× 2 diam.), and interior view of a primaxil (× 3 diam.), on which are seen the articular facets (*IIBr'*) for the secundibrachs; the latter are only partially known. Other letters as usual. (Based on the observations of Jaekel.)

water (Figs. CXXI. and XXXIV.). *Cyathidium*, Steenstrup (1846 ; syn. *Micropocrinus*, Michelin), Uppermost Cretaceous to Miocene, Denmark and Italy. FAMILY 9. EUDESICRINIDAE. Pinnata (?) with patina of 5 RR, enclosing funnel-shaped cavity open below, resting on a solid mass which may represent fused BB or a proximale. Iax articulated to IBr_1, and supporting 2 stout rami which abut on adjoining rami. Axial cords lie close to inner walls of RR. Genera—*Eudesicrinus*, de Loriol (1882) ; and *Cotylederma*, Quenst. (1852 ; syn. *Cotylecrinus*, E. Deslongch.), both Lias. Jaekel would place these genera near the Plicatocrinidae ; they are usually referred to Eugeniacrinidae or Holopodidae.

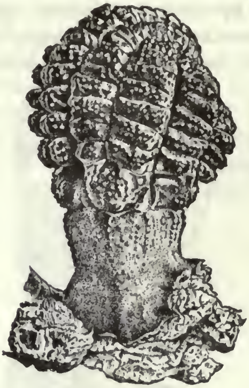


FIG. CXXI.
Adult *Holopus Rangi*, from anterior. (From A. Agassiz, after P. H. Carpenter.) Enlarged by one-twelfth.

ORDER 3. **Dicyclica Camerata**

(= CAMERATA, W. & Sp. *pars*).

Dicyclica in which all IBr and usually IIBr are incorporated in the dorsal cup by iBr, at first loosely, but afterwards by close suture. IBB always the primitive 5. A plate always between r. and l. post. RR, resting on post. B, and followed by others leading up to the anus. Mouth and ambulacra subtegminal. Arms pinnulate.

FAMILY 1. RETEOCRINIDAE. Dicyclica Camerata with RR and Br separated by supplementary plates irregular in size, shape, and arrangement, and forming depressed interradial areas, the posterior of which is divided by a single vertical series of prominent plates leading from post. B to the eccentric anus. Genus—*Reteocrinus*, Billings (1859 ; see W. & Sp., 1897), Ordovician, N. America (Fig. CXXII.) ; 2-3 $\overline{\mathrm{IBr}}$; about 6 $\overline{\mathrm{IIBr}}$, of which the pinnules, borne from $\overline{\mathrm{IIBr}_2}$ onwards, are also fixed in the interradial areas ; the pinnule borne by $\overline{\mathrm{IIBr}_2}$ is in some species represented by a ramus, partly fixed ; the rami may branch again after becoming free, and are uniserial or slightly in zigzag ; tegmen a low dome of minute irregular plates ; stem pentagonal. FAMILY 2. DIMEROCRINIDAE. Dicyclica Camerata with RR in contact except at posterior side, with 2 $\overline{\mathrm{IBr}}$ and a varying number of $\overline{\mathrm{IIBr}}$, separated by a large proximal iBr, which rests on shoulders of RR and supports 2 plates, usually followed by smaller ones merging into iAmb ; post. IR wider, and its proximal plate (anal) supports 3 plates followed by others, and leading up to anus, which has no tube ; iIIBr usually present. Genera—*Ptychocrinus*, W. & Sp. (1885, em. 1897), Ordovician, N. America ; arms fork twice, are slender and uniserial as in *Reteocrinus*. *Orthocrinus*, Jaekel (1895), Devonian, Germany ; arms fork once, are free from Iax, stout and uniserial. *Dimerocrinus*, Phillips (1836 ; synn. *Glyptaster* and *Thysanocrinus*, Hall em. W. & Sp., 1897 ; *Eucrinus*, Ang.), Silurian, Europe and N. America (Fig. CXXIII.) ; arms fork once or twice, are stout, biserial, and directed upwards. *Cyphocrinus*, S. A. Miller (1892 ; syn. *Hyptiocrinus*, W. & Sp.), Silurian, Indiana ; arms fork at least once, are stout, biserial, and pendent, thus exposing the tegmen which is spinous. FAMILY 3. LAMPTEROCRINIDAE. Dicyclica Camerata with a dorsal cup in general structure like that of Dimerocrinidae, but with asymmetry introduced by the development of an anal tube and consequent bulging of IR, and shifting of mouth anteriorly. All from Silurian, N. America. Genera—*Lampterocrinus*, C. F. Roemer (1860, W. & Sp., 1897) ; IBB large, anchylosed ; anal tube central ; arms supposed to be 5 rami bearing alternate ramules, but are not known beyond IIIBr$_1$ (Fig. CXXIV.). *Siphonocrinus*, S. A. Miller (1888, em. W. & Sp., 1897) ; IBB small ; rectum forms an asymmetric protuberance below, then curves subtegminally either to a central anal tube, or right across to an anterior opening at or even beneath the arm-bases.

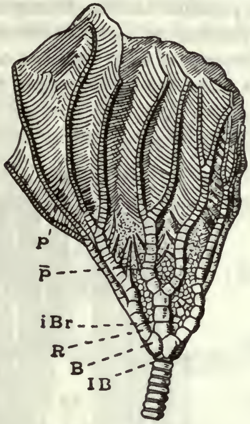


FIG. CXXII.

Reteocrinus Onealli, anterior view. *p*, pinnules ; $\bar{p}$, fixed pinnules ; other letters as usual. (After Wachsmuth & Springer.) × $\frac{3}{2}$.

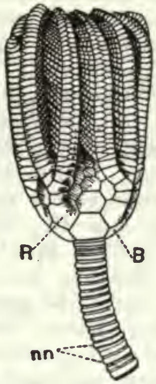


FIG. CXXIII.

Dimerocrinus decadactylus, from Brit. Mus. E6707 ; seen from posterior interradius. *nn*, nodals of stem. × 2 diam.

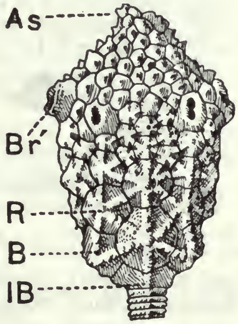


FIG. CXXIV.

Lampterocrinus tennesseënsis, from posterior interradius. *IB*, fused infrabasals ; *Br′*, openings of arm-canals into calyx. (After C. F. Roemer.) × $\frac{3}{4}$.

FAMILY 4. RHODOCRINIDAE. Dicyclica Camerata with RR separated by a single distinct plate in each IR, followed by well-defined iBr regularly arranged (some individuals of *Lyriocrinus* have RR not quite separated, and some species of *Diabolocrinus* have not the single distinct interradial) ; the anal area is not always distinct, and but rarely has a vertical series of plates. $\overline{\text{IBr}}$, 2, in all except the rather doubtful *Anthemocrinus*. Arms free above $\overline{\text{IIBr}}$ (except in *Thylacocrinus*); iIIBr may or may not be present. The plates of the tegmen are small and usually irregular. The family begins in the Ordovician, probably as an independent development from Reteocrinidae or similar forms, and runs parallel to the Dimerocrinidae through the Silurian, but, unlike them, persists to Carboniferous times. There is seen in it an increase in definiteness of iBr, and the origin of biserial arms, which are usually isotomous but exceptionally bear ramules. Genera—*Rhaphanocrinus*, W. & Sp. (1885; syn. *Coelocrinus*, Salter), Ordovician, N. America, Gt. Britain, has uniserial arms and numerous iBr and iIIBr. *Archaeocrinus*, W. & Sp. (1881), Ordovician, N. America, has Br in zigzag, numerous iBr more regular in arrangement, with no vertical series in anal IR (Fig. CXXV.). *Diabolocrinus*, W. & Sp. (1897), Ordovician, N. America, has the larger and more regular iBr surrounded by supplementary plates; the anus is at the end of a strong, subcentral tube; the arms bear ramules. *Lyriocrinus*, Hall (1852; syn. *Marsupiocrinus*, Hall *non* de Blainv. *nec* Phill.), Silurian, N. America and England, has but 2 rami to each ray, biserial; iBr, 1 + 2 + 1, not always quite separating RR; anal area usually of similar structure. *Anthemocrinus*, W. & Sp. (1881). Silurian, Gotland, has only one IBr, and the first large iBr is followed by only 1 or 2 small ones; the biserial arms fork 2 or 3 times. *Diamenocrinus*, Oehlert (1891, em. Jaekel, 1895), Devonian, France and Germany, has repeatedly isotomous arms, with Br in zigzag; 6-8 $\overline{\text{IIBr}}$, and a long narrow series of iBr. *Thylacocrinus*, Oehlert (1878), Devonian, France and New York (Fig. CXXVI.), has arms fixed up to IIIBr and sometimes IVBr, after which follow long unbranched biserial rami; supplementary plates occur between all fixed brachial series; stem minute or (?) absent. *Lahuseniocrinus*, Tschernyschew (1892,-93), Lower Devonian, Ural, appears allied to the preceding, but base and free brachials are unknown.

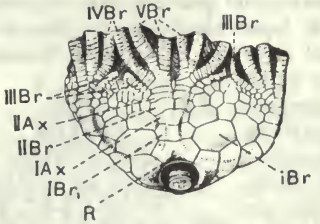


Fig. CXXV.

Archaeocrinus desideratus, from the left posterior radius. (Diagrammatised from Wachsmuth & Springer.) × ½.

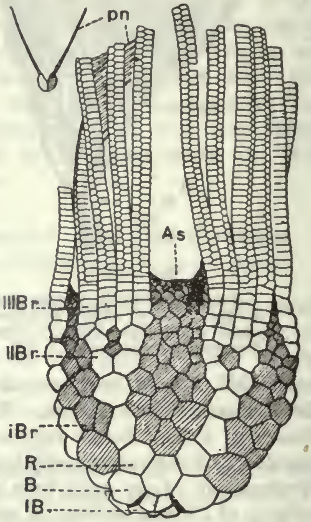


Fig. CXXVI.

Thylacocrinus Vannioti (from Brit. Mus. E6642). Seen from posterior interradius. Owing to slight crushing all five infrabasals (*IB*) are seen, and the absence of a stem-facet may be noted. Supplementary plates are shaded. The section of an arm with pinnules (*pn*) is after Oehlert. × ¾.

Rhipidocrinus, Zittel (1879, ex Beyrich, MS.), Devonian, Germany, has stout uniserial rami giving off biserial ramuli on alternate sides. *Acanthocrinus*, C. F. Roemer (1850, em. Jaekel, 1895), Devonian, Germany, does not differ greatly from the next genus. *Rhodocrinus*, J. S. Miller (1821, restricted W. & Sp., 1881), Carboniferous and (?) Devonian, Europe and N. America; has a vertical series of anals and isotomous arms, all the free parts of which or only the finials are biserial. *Condylocrinus*, Eichwald (1859, em. Tschernyschew, 1893), Lower Devonian, Ural, differs, if at all, in iBr series, which runs—1, 1, 2, 3. *Ophiocrinus*, Salter (1856; *non* Charlesworth, *nec* Semper, *nec* Angelin), Devonian, S. Africa, has numerous iBr and several iIIBr; IIIBr free and in zigzag. *Gilbertsocrinus*, Phillips (1836; synn. *Ollacrinus*, Cumberland MS.; *Goniasteroidocrinus*, Ly. & Cass.; *Trematocrinus*, Hall), Devonian and Carboniferous, Europe and N. America (Fig. CXXVII.), distinguished by small pendent arms, and large, branching, horizontal, hollow extensions of the interambulacral areas of the tegmen, of uncertain function.

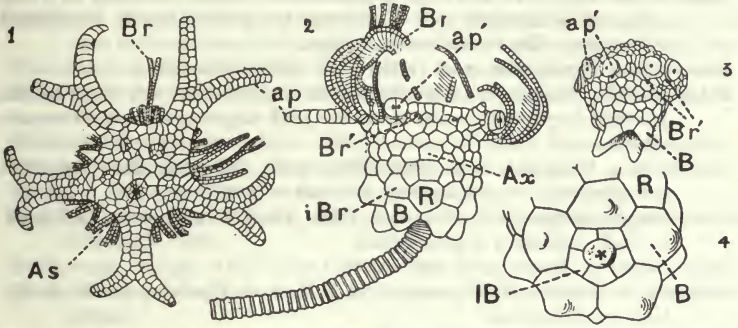


FIG. CXXVII.

Gilbertsocrinus. 1, *G. lyonanus* (=*G. dispansus*, W. & Sp.), ventral view, showing the tegminal appendages and the proximal portions of the arms emerging from beneath them. 2, *G. tuberculosus*, the appendages mostly broken off, but more of the arms preserved. 3, *G. calcaratus*, showing how the appendages of the European forms are double where they issue from the tegmen. 4, *G. typus*, patina from below; *ap*, tegminal appendages; *ap'*, their points of origin, showing central canal; *Ax*, primaxil; *Br*, pinnulate arms, which issue from the dorsal cup at *Br'*. Other letters as usual. (All after Wachsmuth & Springer.) × ⅔.

The following **incorrect** or **indeterminable Names** may be added to those already quoted as synonyms or *incertae sedis*:—

Adelocrinus, Phillips (1841), Devonian, Britain, is probably syn. of either *Hexacrinus* or *Arthracantha* (see Whidborne, 1899).

Allionia, Michelotti (1861), syn. of *Antedon*.

Aporocrinus, Austin (1842), is an Agelacrinid, *fide* label on *A. gyratus* in Bristol Museum.

Aspidocrinus, Hall (1859), Silurian, New York; encrusting root of a crinoid.

Asteria, Auctt. vett., a Pentacrinoid columnal (=*Pentacrinos*, Agricola).

Asterias, Linn. *pars* (1758); syn. of *Antedon* and *Actinometra*.

Asteriatites, Schloth. (1813); *A. pennatus* and *A. rosaceus*, syn. of *Antedon*.

Asterocrinus, Münster (1838), "aus dem Orthoceratiten-kalk bei Elbersreuth," if a Crinoid at all, is an Inadunate.

Astrios, Troost, nom. nud. (1850) ; not known.

Astrocoma, de Blainville (1830) ; syn. of *Antedon* and *Actinometra.*

Astrocrinus, Cumberland (1829), *fide* Wachsmuth & Springer, not known.

Astropodia, Llhuyd et Auctt. pre-Linn., for Crinoid arms ; but Ure (1797) applied it also to various cup-plates, and Defrance (1819) to *Apiocrinus.*

Atocrinus, M'Coy (1844 or 1862), Carboniferous, Ireland ; referred to *Platycrinus* by de Koninck & C. F. Roemer, to *Cyathocrinus* by Wachsmuth & Springer. The former probably right.

Balanocrinus, Troost, nom. nud. (1850) ; syn. of *Lampterocrinus.*

Bohemicocrinus, Waagen & Jahn (1899), Silurian, Bohemia ; cup alone known, probably *Carpocrinus* or *Desmidocrinus ;* RR shaped much as in *Barrandeocrinus.*

Caleidocrinus, Waagen & Jahn (1899), Ordovician, Bohemia ; like *Taxocrinus*, but apparently no anal between RR, and no anal ridge.

Calocrinus, Steininger (1849), Devonian, Eifel. Dicyclic Inadunate ; IBB fused ; no anal ; perhaps a *Cupressocrinus.*

Campanulites, G. Troost, nom. nud. (1850).

Centrocrinus, Worthen (1890), *non* Austin & Meek & Worthen, *nec* W. & Sp. ; ? syn. of *Gazacrinus.*

Codonocrinus, Troost, nom. nud. (1850) ; syn. of *Pterotocrinus*, *apud* Shumard (1866).

Comatulina, d'Orbigny (1852), Oxfordian, *C. costata* = *Solanocrinus*, Goldf., which is syn. of *Antedon.*

Comaturella, Münster (1839) ; syn. of *Antedon.*

Conocrinus, Troost, nom. nud. (1850) ; syn. of *Alloprosallocrinus*, *apud.* W. & Sp.

Cophinus, Murchison, ex König MS. (1839), Silurian, England. Impressions of stems.

Crumenaecrinus, Troost, nom. nud. (1850).

Cupulocrinus, d'Orb. (1850), based on *Scyphocrinus heterocostalis*, Hall (1847), which is referred by Wachsmuth & Springer to Flexibilia Impinnata.

Cypressocrinus, a variant and possibly preferable spelling of *Cupressocrinus.*

Cystocrinus, C. F. Roemer (1860), Silurian, Tennessee. Stem only known, see Fig. L. 2.

Daemonocrinus, Troost, nom. nud. (1850) ; syn. of *Pterotocrinus*, *apud* Shumard (1866).

Decacnemos, Bronn ex Linck (1837) ; syn. of *Antedon.*

Decadactylocrinus, D. D. Owen, nom. nud. (1843) ; syn. of *Heterocrinus*, *apud* Shumard (1866).

Decameros, d'Orbigny ex Linck (1850) ; syn. of *Antedon.*

Dimorphicrinus, d'Orbigny (1849), based on *Platycrinus pentangularis*, Miller ; syn. of *Orophocrinus*, p. 84.

Doliolocrinus, Troost MS., *fide* Hall (1858) ; *D. ovalis* is syn. of *Dichocrinus simplex*, Shumard.

Donacicrinus, Troost, nom. nud. (1850).

Echinocrinus, L. Agassiz, 1841, and T. & T. Austin (1842) ; not a crinoid, but an echinoid = *Archaeocidaris*, M'Coy, 1844.

Emperocrinus, Miller & Gurley (1895), Silurian, Indiana ; probably syn. of *Anthemocrinus ;* but has 3 IBB, and was placed by its authors with doubt in Taxocrinidae.

Encrinos, Agricola (1558), a stem-fragment composed of *Pentacrini* or *Asteriae* (*q.v. supra*).

Entrochus, Agricola (1558), a stem-fragment composed of Trochitae (*q.v. infra*).

Ganymeda, J. E. Gray (1834); centrodorsal of *Antedon*, *apud* L. Agassiz (1841).

Gaurocrinus, S. A. Miller (1883), Ordovician, N. America; referred by Wachsmuth & Springer part to *Reteocrinus*, part to *Ptychocrinus*.

Glenotremites, Goldfuss (1832), centrodorsal of *Antedon*.

Gnathocrinus, T. & T. Austin, nom. nud. (1842). The genotype *G. fusiformis* is proved by Austin's MS. drawings to be syn. of *Millericrinus Pratti*.

Goldfussia, Norman (1891, *non* Castelnau, 1843), proposed for *Comatula* vel *Comaster multiradiata*, Goldf. *non* Linn., *nec* Lam., a quite unrecognisable form.

Grammocrinus, Eichwald (1859), Ordovician; columnals incertae sedis.

Halophenix "of our British Museum," *fide* Cumberland (1826); syn. of *Pentacrinus*.

Helmintholithus entrochus, Linn. (1768); stems of various Palaeozoic Crinoids.

Helmintholithus portentosus, Linn. (1768); syn. of *Pentacrinus*.

Hertha, v. Hagenow (1840); centrodorsal of *Antedon*.

Icosidactylocrinus, D. D. Owen, nom. nud. (1843); referred to *Glyptocrinus* by Shumard (1866).

Kallispongia, Wright (1877); larva of *Antedon*.

Koninckocrinus, Seeley, nom. nud. (1864); syn. of *Torynocrinus* and *Acrochordocrinus*.

Medusacrinus, T. & T. Austin, nom. nud., *fide* Wachsmuth & Springer (1881).

Microcrinus, Emmons (1858), Eocene, N. Carolina; probably centrodorsal of *Atelecrinus*.

Mitrocrinus, Miller & Gurley (1894), Ordovician, Tennessee; based on a six-rayed individual, probably abnormal, and a Periechocrinid or Carpocrinid.

Pachyantedon, Jaekel (1891), Upper Cretaceous, N. Germany. Based on impression of stout arms, and a few cirri; Br and cirrals in zigzag.

Pachycrinus, Eichwald (1840), Carboniferous, Russia; columnals only, in part a syn. of *Platycrinus* (see p. 132).

Pachyocrinus, E. Billings (1859), Ordovician, Canada; founded on a single base, with no diagnostic features.

Pentagonites, Rafinesque (1819), based on pentagonal columnals, probably of a Heterocrinid.

Perischodomus magnus, Tornquist (1894); syn. of *Adelocrinus hystrix*, Phill.

Petinocrinus, Hall (1859), Geol. Iowa, vol. i. Suppl. p. 49. Not seen.

Phialocrinus, Eichwald (1860), Ordovician, Russia; encrusting roots with ridged under surface (see p. 133).

Platysphaerites, Trenkner (1868), doubtfully crinoidal.

Proteuryale, J. Müller ex C. F. Roemer MS. (1855); syn. of *Cylicocrinus confluentinus*, *apud* Jaekel (1895).

Pterocoma, L. Agassiz (1835); syn. of *Antedon*.

Rhodocalix, Trenkner (1868), doubtfully Crinoidal.

Shumardocrinus, Miller & Gurley (1895), based on imperfect specimens of *Steganocrinus concinnus*.

Solacrinus, L. Agassiz (1835), for *Solanocrinus*, Goldf. (1832), which is syn. of *Antedon*.

Sphenocrinus, Eichwald (1856), quinquepartite columnals.

Sycocrinus, T. & T. Austin (1843); the authors' MS. drawings suggest that *S. clausus* = *Lageniocrinus*, *S. Jacksoni* = *Cryptocrinus*, and *S. anapeptamenos* = *Hypocrinus*.

Syringocrinus, E. Billings (1859), Ordovician, Canada; stem of *Dendrocystis*.

Tetracrinus, T. & T. Austin, nom. nud. (1842, *non* Münster). Not known.

Tetramerocrinus, T. & T. Austin (1843); shown by labels and MS. to be syn. of *Melocrinus* or *Mariacrinus*.

Thalamocrinus, Miller & Gurley (1895), Silurian, Tennessee. Cup alone known; like *Bactrocrinus* or *Homocrinus*, without RA.

Trianisites, Rafinesque, *fide* L. Agassiz (1841); not known.

Triplaricrinus, Goldfuss, MS. label for *Hexacrinus pateraeformis*, *fide* L. Schultze (1867).

Trochitæ, Auctt. vett., a round columnal with radiating striae.

Vletavicrinus, Waagen & Jahn (1899), Silurian, Bohemia; if monocyclic, must be a Batocrinoid; and if each Br bears more than one pinnule, is probably a Carpocrinid.

Xenocrinus, Jahn (1892) *non* Miller; altered to *Zenkericrinus*, Waagen & Jahn (1899), Silurian, Bohemia; based on an imperfect cup, which does not differ from *Mariacrinus* (p. 161).

A few of the **Terms used by some other writers**, and not previously alluded to, may be correlated with those of the present work:—

Subradialia, de Koninck and Americans = BB of Dicyclica.

Subradiale, Jaekel = RA [and presumably all R*i*] in Monocyclica Inadunata.

Subanale, Jaekel = RA in Dicyclica Inadunata.

Azygos plates, Billings et alii = anals in general, and RA in particular.

Costalia = IBB in *Marsupites* (J. S. Miller); IBB & BB in *Dendrocrinus* (Hall); BB in clearly dicyclic Inadunata and Flexibilia, and in *Dimerocrinus* (J. S. Miller, Hall); BB of all Crinoidea (Lovén); R*i* in *Heterocrinus* (Hall); RR in *Scyphocrinus*, *Lyriocrinus*, *Macrostylocrinus* (Hall); RR & $\overline{\mathrm{IBr}}_1$ in monocyclic or pseudomonocyclic Camerata and Articulata (J. S. Miller, Hall); RR & $\overline{\mathrm{IBr}}$ in Cladocrinoidea only (Jaekel); IBr in all Crinoidea (Bather in earliest papers; Wachsmuth & Springer, 1897); iBr$_1$ in *Eucalyptocrinus* (Hall).

Scapula, J. S. Miller, Hall; *Radiale articulare*, L. Schultze, Zittel = the proximal plate in a ray that has an articular facet for the arms, therefore may be R, IBr$_1$, IBr$_2$, or IAx.

Radialia, Müller, Zittel; *Primary Radials*, Wachsmuth & Springer (1879-81) = all plates in a ray up to first forking, *i.e.* R & IBr up to IAx.

Brachialia of 1st, 2nd, 3rd, etc. order, Müller, Zittel, Wachsmuth & Springer before 1890; *articles brachiaux*, de Koninck = free Br only.

Brachialia, *Dibrachialia*, *Tribrachialia*, Jaekel = IBr, IIBr, IIIBr.

Brachialia, P. H. Carpenter, before 1890 = Finials.

Radialia distichalia or *Distichalia*, Müller, Zittel, Waagen & Jahn; *Secondary Radials*, Wachsmuth & Springer (1879-81); *Dicostalia*, Jaekel = $\overline{\mathrm{IIBr}}$.

Distichalia, P. H. Carpenter (1879), Wachsmuth & Springer (1897) = IIBr., fixed or free.

Palmaria, Huxley (1877), P. H. Carpenter (1879), Wachsmuth & Springer (1897) = IIIBr.

Postpalmaria of 1st, 2nd, 3rd, etc. order, Carpenter, Wachsmuth & Springer (1897) = IVBr, VBr, VIBr, etc.

The corresponding terms for supplementary plates—*Intercostal*, *Interscapular*, *Interradial*, *Interaxillary*, *Interdistichal*, *Interpalmar*, and *Interbrachial*—have also been used in diverse senses.

For **Literature** of Crinoidea see p. 211.

CHAPTER XII.

THE EDRIOASTEROIDEA.[1]

CLASS IV. EDRIOASTEROIDEA, E. BILLINGS (1854,-58; HUXLEY, 1877; and BATHER, 1899)

(=THYROIDA, Chapman, 1860; AGELACRINOIDEA, S. A. Miller, 1877-83; Worthen, 1883; CYSTASTEROIDEA, Steinmann, 1888; F. Bernard, 1893; THECOIDEA, Jaekel, 1895).

Not divided into Orders.

PELMATOZOA in which the theca is composed of an indefinite number of irregular plates, some of which are variously differentiated in different genera; with no subvective skeletal appendages, but with central mouth, from which there radiate through the theca five unbranched ambulacra, composed of a double series of alternating plates (covering-plates), sometimes supported by an outer series of larger alternating plates (side-plates or flooring-plates). Pores between (not through) the ambulacral elements, or between them and the thecal plates, permitted the passage of extensions from the perradial water-vessels. Anus in posterior interradius, on oral surface, closed by valvular pyramid. Hydropore (usually, if not always, present) between mouth and anus.

Reducing the characters of the Edrioasteroidea to their simplest expression, one may imagine a schematic type of the following nature:—A flexible theca of sack form, composed of numerous irregular, polygonal plates deposited in the integument, probably with the stroma-strands between them still plainly visible (cf. *Stromatocystis*); it would have a mouth in the centre of the upper surface, and would be attached by some indefinite portion of the lower surface; the anus, with its valvular covering, would lie on the upper surface, and there would probably be a hydropore between it and the mouth. So far this type would present primitive characters like those of the earlier Amphoridea, from which one may suppose it to have been derived. But the structure and relations of the ambulacra, even in their least specialised form, at once remove the type from primitive simplicity, and place it on a road different from that traversed by other Pelmatozoa. The evidence suggests the existence of a circumoesophageal water-ring, with five perradial canals, and their associated nerves and blood-vessels, passing between or below the thecal plates, and underlying a ciliated food-groove, which was covered by an alternating series of movable plates (covering-plates = ambulacrals of Crinoidea, but probably not those of Echinoidea and Asteroidea). Pores between the plates lining or flooring the groove (adambulacrals of Pelmatozoa, but perhaps = superambulacrals of Asteroidea) permitted the passage either of podia or ampullae. In Cystidea, Blastoidea, and primitive Crinoidea, on the other hand, there was a free exit for the ambulacral organs only through the peristome; in fact, Blastoidea and Cystidea present no evidence that they possessed perradial water-vessels and podia at all.

---

[1] By F. A. Bather, M.A.

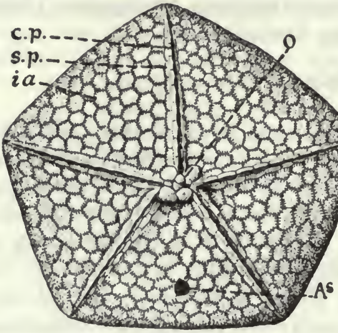


Fig. I.

Stromatocystis pentangularis, oral surface. *As*, anus; *O*, peristomial plates; *c.p*, covering-plates; *s.p*, side-plates; *ia*, interambulacrals. (Reconstructed from Pompeckj's figures.) Slightly enlarged.

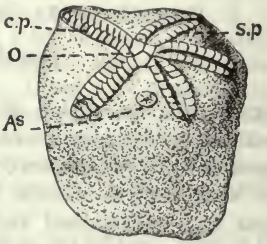


Fig. II.

Cystaster granulatus, from posterior, showing oral surface in perspective. The two left-hand rays retain the covering-plates, which are lost from the others. Lettering as in Fig. I. (Reconstructed from Hall's figures.) × 3 diam.

The primitive sack form did not long persist, but the following characters were, as a rule, impressed upon it: a sessile habit, the consequent assumption of a circular, flattened form, the differentiation of the upper and under surfaces, the development of marginals or concentric frame-plates, and the tendency to increase the food-gathering surface by spiral coiling of the ambulacra in either sinistral or dextral direction. According to the varied extent of these several modifications, the Edrioasteroidea are divisible into 3 families—Agelacrinidae, Cyathocystidae, Edrioasteridae. But to these must be added a fourth, Steganoblastidae, in which the development of a short stem was correlated with greater concentration and regularity of the thecal elements.

Family 1. Agelacrinidae. Edrioasteroidea with a theca composed mostly of thin plates, flexible, attached temporarily or permanently by the greater part of the aboral surface ; with ambulacra confined to the oral surface. Genera—*Stromatocystis*, Pompeckj (1896), Cambrian, Bohemia, seems to have had a somewhat flexible theca of non-imbricate plates (Fig. I.). Rays straight and extending to the margin, imposing on the theca a subpentagonal outline ; composed of stout and long alternating side-plates, along the outer margins of which are pores [for podia ?] while along their inner margins is a groove, protected by minute covering-plates. Four large and many small plates [modified side- and covering-plates] surround and cover the mouth. Interambulacrals hexagonal, united by stroma-strands. Under side of theca composed of irregular plates, without evidence of stroma-strands, and larger towards the middle. The animal was probably sessile on its under surface, but perhaps not fixed permanently. *Cystaster*, Hall (1872, *Thecocystis*, Jäk.), Ordovician, Ohio, is also primitive (Fig. II.). Theca sac-like, composed of minute plates, not always attached (?) ; rays straight, composed of alternating covering-plates supported on side-plates ; no hydropore observed. *Hemicystis*, Hall (1852), Ordovician and Silurian, N. America and Bohemia, shows an advance on *Cystaster* in the imbrication of the thecal plates, and their differentiation into larger interambulacrals, and a zone of smaller marginals. This leads on to *Agelacrinus* and its allies *Streptaster* and *Lepidodiscus*, all which are characterised by the curvature of the rays, sinistrally, dextrally, or both, by the elaboration of the marginal zone, and by their flattened sessile habit, being usually attached to brachiopod shells. The type-species of *Agelacrinus* is the Devonian *A. hamiltonensis*, Vanuxem (1842), (Fig. III.), in which the anterior and two left-hand rays curve sinistrally, the two others dextrally ; the interambulacrals are large, non-imbricate, and radiately ridged ; there is a border of large plates, with an outer

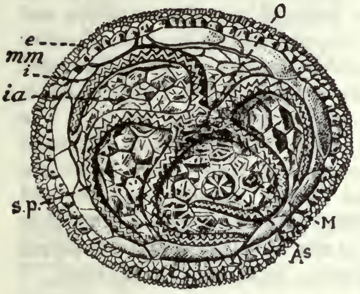


Fig. III.

Agelacrinus hamiltonensis, oral surface. *mm*, marginals, consisting of the large internal (*i*) and the small external (*e*) ; *M*, supposed madreporite. Other letters as before. (After Hall.) × $\frac{3}{2}$.

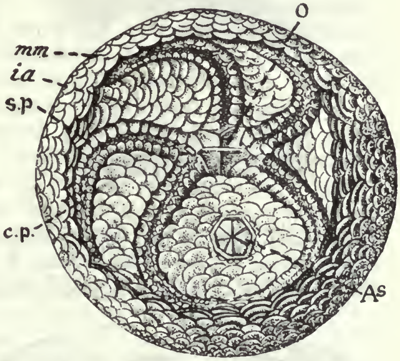


Fig. IV.

Lepidodiscus cincinnatensis, oral surface. Lettering as before. (After Hall.) × $\frac{5}{2}$.

border of small plates. *Lepidodiscus*, Meek & Worthen (1868), Ordovician to Carboniferous, has imbricating interambulacrals and a border of small imbricating plates; plates forming the floor of the ambulacra, and a pentagonal internal frame around the mouth, have been described by Miller & Faber (1892), but more details are needed; Hall figures right posterior ray as dextral, and the rest as sinistral (Fig. IV.); other arrangements may obtain, but the rays adjacent to the anus always curve towards it. The Devonian *Haplocystis*, C. F. Roemer (1855), is known from an internal cast, apparently proving that the ambulacra were floored by a single row of plates [? fused adambulacrals], between the edges of which were pores [for passage of podia]. The Ordovician *Streptaster*, Hall (1872), has all its rays sinistral. *Discocystis*, Gregory (1896), based on *Echinodiscus optatus*, Worthen & Miller, is doubtful.

FAMILY 2. CYATHOCYSTIDAE. Edrioasteroidea with the theca composed on the oral surface of five deltoids surrounded by marginals, but below of a fused solid mass of stereom, with irregular longitudinal sutures; permanently attached by the aboral surface as by an encrusting root; ambulacra confined to oral surface. Genus—*Cyathocystis*, Schmidt (1880), Ordovician, Esthonia (Fig. V.), is not far removed from *Stromatocystis* and *Cystaster*, but the trend of its evolution is quite away from that of either *Edrioaster* or *Agelacrinus*. Upper ambulacral surface of theca bordered by a pentagonal frame of 40 marginals; rays straight, with a single series of covering-plates; five larger plates cover the mouth. The minute plates that formed the theca of *Cystaster* are here fused into solid masses; thus there arise between the ambulacra 5 large Δ, and below the marginals a massive cup, fixed to some foreign body by its base, and occasionally marked by obscure longitudinal sutures, irregular in number and position, but never more than 5. Anus, with pyramid of 5 plates, lies between a Δ and the adjacent marginals; no hydropore observed.

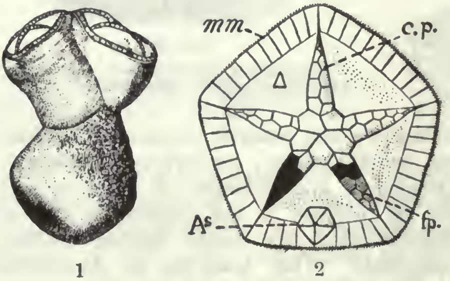


FIG. V.

Cyathocystis Plautinae. 1, two individuals growing on a pebble of rolled coral, and seen from the side. (After Schmidt.) Nat. size. 2, oral surface. *As*, anus; Δ, interambulacrals fused into deltoids; *mm*, marginals; *c.p*, covering-plates, partly removed from the posterior rays exposing *fp*, which are not a distinct series of flooring-plates, as represented, but ledges projecting from the under side of the deltoids. (Diagrammatised from Schmidt.) × 3 diam.

FAMILY 3. EDRIOASTERIDAE. Edrioasteroidea with flexible theca composed of thin plates; attached, if at all, by a small central portion of the excavate aboral surface; ambulacra pass on to aboral surface. Genera—*Aesiocystis*, Miller & Gurley (1894), Ordovician, Kentucky, has a subpentagonal theca, with height two-thirds the width; rays wide and straight, with large covering-plates; interambulacrals non-imbricate. Podial pores, madreporite, and abactinal surface unknown; but the genus appears to connect this family with the more primitive forms of Agelacrinidae. *Edrioaster*, Billings (1858), Ordovician, Canada (Fig. VI.), also includes "*Agelacrinites Buchianus*," Forbes (1848), from Wales. Theca about half as high as wide, depressed slightly at oral pole. Rays curved, all or some sinistral or dextral, passing on to under surface of theca; ambulacral groove floored by alternating plates [? adambulacrals], between which were pores [? for podia]; with covering-plates, *i.e.* ambulacrals, over the groove. Interambulacrals non-imbricate. Under-surface of theca excavate, its central region composed of a flexible membrane set with minute imbricating plates, and in a frame of about 11 large plates. Whether the animal was attached by the central part of this membrane is doubtful; immediately round the centre this is evaginated in five lobes, apparently caused by the pressure of some internal organs [? gonads], which must have acquired pentamerous symmetry. *Dinocystis*, Bather (1898), Uppermost Devonian, Belgium, has a slighter frame on the aboral surface, and the surrounding region composed of a thin flexible integument containing narrow imbricating ossicles; otherwise like *Edrioaster*.

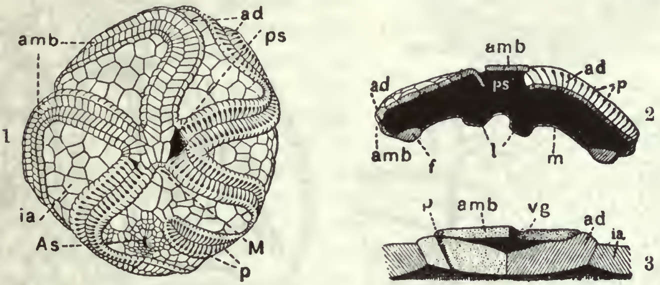


Fig. VI.

Edrioaster Bigsbyi. 1, oral surface, with covering-plates (*amb*) on the anterior and left anterior grooves, but removed from the others, which show only the side- or flooring-plates (*ad*), between which are pores (*p*). The greater part of the subpentagonal peristome (*ps*) is roofed by enlarged covering-plates. *ia*, interambulacrals, one of which is a madreporite (*M*). 2, section across the same specimen through the right anterior radius and left posterior interradius. The covering-plates are removed except just over the peristome, and in the ambulacrum seen in section on the left. *f*, frame of stouter plates; *m*, membrane with imbricating plates, thrown into five lobes (*l*). 3, section across an ambulacrum, with plates *in situ* covering ventral groove (*vg*). Dotted surfaces are the natural edges of the plates, ruled surfaces are cut through the plates. (All slightly diagrammatised from a specimen belonging to the Canadian Geological Survey.) 1 and 2 are nat. size.

Family 4. Steganoblastidae. Edrioasteroidea, with a rigid theca composed of plates relatively larger and thicker than in other families of this class; these include elements comparable to the RR and BB of Blastoidea; BB attached to a stem, probably short; ambulacra descend into the radials. Genus—*Steganoblastus*, Whiteaves (1897, originally described as *Astrocystites*, name preoccupied), Ordovician, Canada (Fig. VII.). The remarkable resemblance to *Asteroblastus*, insisted on by its founder, suggested the reference of *Steganoblastus* to the Protoblastoidea (Bather, 1899); but the ambulacra are now known to have essentially the same structure as in *Edrioaster*, while the absence of brachioles may be maintained with confidence. Theca piriform, its plates strongly marked with axial folds, and consisting of: BB (5 ?, sutures not clear); RR, 5, alternating with BB, and receiving the distal ends of the ambulacra; interambulacrals, one large one and an uncertain number of smaller ones, in each interradius; 5 slightly-pitted plates of spear-head shape, stretching up between the ambulacra to the oral pole and simulating O of Crinoidea or Δ of Blastoidea, but perhaps being only proximal covering-plates. The anus pierces one interambulacrum, and slightly disturbs the pentamerous symmetry of the theca. From the mouth 5 ambulacra stretch about half-way down the theca; the adambulacrals (side- or flooring-plates) appear almost anchylosed, but the pores between them are very clear, and one can trace the original median line of suture; the ambulacrals or covering-plates were stout, at least in the proximal regions, where they seem to have combined with the spear-head plates to form a solid roof over mouth and food-grooves. Stem small, round, with lumen less than half the diameter. Fifty years ago *Steganoblastus* would have been described as a generalised or synthetic type, with Cystid, Blastoid, Crinoid, and Asteroid affinities; it is simpler to regard it as a specialised Edrioasteroid, in which features common in stalked genera of other classes have been evolved independently under similar conditions of existence.

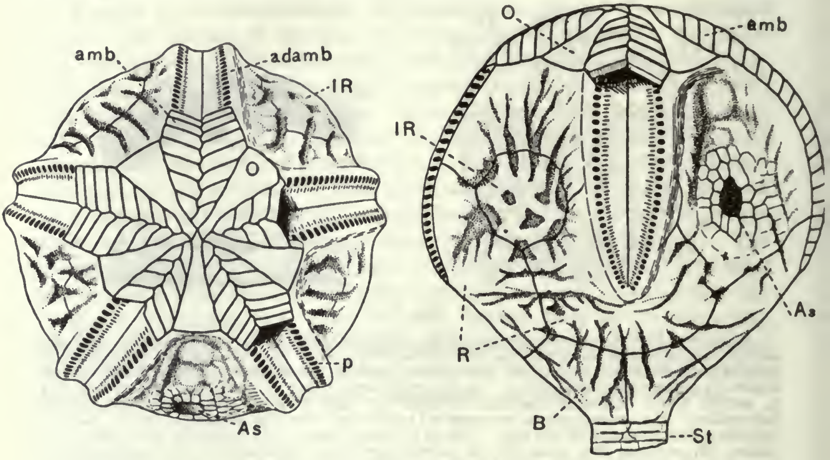


Fig. VII.

Steganoblastus ottawaensis, slightly restored from the type-specimens, and × 3 diam. 1, oral surface; 2, from l. post. radius. *adamb*, adambulacrals or side-plates; *amb*, ambulacrals or covering-plates, mostly removed; *As*, anus surrounded by small plates; *B*, basal; *IR*, large median interradial; *O*, 5 orals or proximal ambulacrals; *p*, pores between side-plates; *R*, radial; *St*, fragment of stem.

Cyclocystoides, Billings and Salter (1858), Ordovician of N. America and Britain (Fig. VIII.), probably belongs to this class, though not to any of the recognised families. It is hardly well enough known to make the type of an order as yet. A ring of stout ossicles, more regular than that seen in *Agelacrinus* and *Edrioaster*, forms a frame between which are stretched two thinly plated membranes, rarely preserved. The dorsal membrane contains irregular non-imbricating plates (Miller & Faber, 1892). The plates of the ventral membrane (*apud* J. Hall, 1866) were delicately reticulate, and arranged in numerous rays passing from a central pyramid of minute plates [mouth ?]. Eccentrically, between two rays, is an oval opening [anus ?]. Outside the frame is a border of smaller plates as in *Agelacrinus.* The animal was not permanently sessile [but could probably fix itself like a limpet].

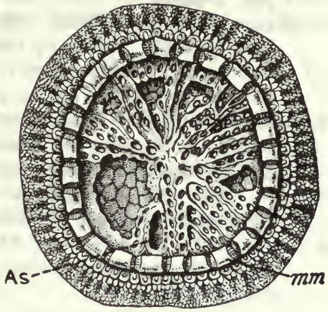


Fig. VIII.

Cyclocystoides Salteri. *As*, supposed region of anus; *mm*, frame of larger marginals. The plated aspect of the flooring, as seen through the openings, is based on Miller & Faber; otherwise the figure is copied from Hall. × ½.

The classificatory position here assigned to the Edrioasteroidea is not that usually accepted by zoologists, although many have given them equal, nearly equal, or greater classificatory value under various names (see heading, p. 205). Whatever may eventually prove to be the value of the characters insisted on in the present work or in others, even if there be traced a closer connection with Diploporita than is as yet apparent, the Edrioasteroidea can never be thought a less distinct or less homogeneous group than, say, the Blastoidea. The zoological importance of the Edrioasteroidea is another reason for raising them to this position. Many zoologists, *e.g.* Forbes, Billings, Neumayr, Steinmann, have regarded them as connecting either the Echinoidea or the Asteroidea with the Cystidea. On the hypothesis, ever becoming more probable, that all eleutherozoic Echinoderms are descended from some pelmatozoic ancestor or ancestors, then the Edrioasteroidea are alone among Pelmatozoa in presenting a type of ambulacrum from which the holothurian, stellerid, and echinoid types may readily be derived.

Literature of Pelmatozoa.

1. *Agassiz, A.* 1892. (*Calamocrinus Diomedae* . . . with notes on the apical system and the homologies of Echinoderms.) Mem. Mus. Comp. Zool. Harvard, vol. xvii., No. 2, 95 pp., xxxii. pls.
2. *Angelin, N. P.* 1878. Iconographia Crinoideorum in Stratis Sueciae Siluricis Fossilium, 4to, iv. and 62 pp., xxix. pls. Holmiae.
3. *Austin, T. and T.* 1843. (Descriptions of several new genera and species of Crinoidea.) Ann. Mag. Nat. Hist. (1) vol. xi. pp. 195-207. (Palaeozoic Crinoids and Blastoids.)
4. —— 1843-1849. Monograph on recent and fossil Crinoidea, 4to, 128 pp., xvi. pls., London and Bristol.

5. *Barrande, J.*, continued by *Waagen, W. and Jahn, J. J.* 1887,-99. Système Silurien . . . de la Bohême. Recherches Paléont., vol. vii. Echinodermes. I. Cystidées, xvii. + 233 pp., xxxix. pls. II. Crinoïdes, vi. + 216 pp., xl. pls. Prague.

6. *Bather, F. A.* 1890-1892. (British Fossil Crinoids, i.-viii.) Ann. Mag. Nat. Hist. (6), vol. v. pp. 306-334, pl. xiv., 373-388, pl. xv., 485, 486 ; vol. vi. pp. 222-235, pl. x. ; vol. vii. pp. 35-40, pl. i., 389-413, pl. xii. ; vol. ix. pp. 189-236, pls. xi.-xiii. (Inadunata, chiefly Silurian.)

7. —— 1893. (The Crinoidea of Gotland. Part I. The Crinoidea Inadunata.) K. Svenska Vet.-Akad. Handl. vol. xxv. No. 2, 200 pp., x. pls. (All Silurian ; with Bibliography.)

8. —— 1896. (*Uintacrinus:* a morphological study.) Proc. Zool. Soc. London, for 1895, pp. 974-1004, pls. liv.-lvi.

9. —— 1897. (*Hapalocrinus Victoriae*, n.s., Silurian, Melbourne, and its relation to the Platycrinidae.) Geol. Mag., n.s., dec. iv. vol. iv. pp. 337-345, pl. xv.

10. —— 1898-99. (Wachsmuth and Springer's Monograph on Crinoids.) Geol. Mag., n.s., dec. iv. vols. v., vi. ; also separately published, London. (The separate issue contains a Bibliography of Wachsmuth.)

11. —— 1898-99. (Studies in Edrioasteroidea.) Geol. Mag., n.s., dec. iv. vols. v. and vi. In progress.

12. —— 1899. (A phylogenetic classification of the Pelmatozoa.) Rep. Brit. Assoc. for 1898, pp. 916-923.

13. *Beyrich, H. E.* 1858. (Ueber die Crinoiden des Muschelkalks.) Abh. Akad. Wiss. Berlin, Phys. Klasse, 1857, pp. 1-49, pls. i.-ii.

14. —— 1871. (Ueber die Basis der Crinoidea Brachiata.) Monatsber. Akad. Wiss. Berlin, pp. 33-55. Translation in Ann. Mag. Nat. Hist. (4), vol. xi. pp. 393-411.

15. *Billings, E.* 1858. (On the Cystideae of the Lower Silurian rocks of Canada.) Canadian Organic Remains, dec. iii. pp. 9-74, pls. i.-vii., Montreal.

16. —— 1859. (On the Crinoideae of the Lower Silurian rocks of Canada.) *Op. cit.*, dec. iv. pp. v., vi., and 7-66, pls. i.-x.

17. —— 1869-70. (Notes on the structure of the Crinoidea, Cystidea, and Blastoidea.) Amer. Journ. Sci. (2), vol. xlviii. pp. 69-83 ; xlix. pp. 51-58 ; and l. pp. 225-240, and 436. Reprint in Ann. Mag. Nat. Hist. (4), vol. v. pp. 251-266, 409-416, and vii. 142-158 ; and in Palaeozoic Fossils, vol. ii. pp. 90-128, Montreal.

18. *Billings, W. R.* 1881-87. Various papers in Trans. Ottawa Field-Nat. Club, vols. i. and ii. ; and Ottawa Naturalist, vol. i. (Cystids and Crinoids.)

19. *Buch, C. L. von.* 1845. (Ueber Cystideen eingeleitet durch die Entwickelung der Eigenthümlichkeiten von *Caryocrinus ornatus*, Say.) Abhandl. Akad. Wiss. Berlin, Phys. Kl., 1844, pp. 89-116, pls. i. and ii. Translation in Quart. Journ. Geol. Soc. London, vol. ii., part ii., pp. 20-42, pls. iii., iv.

20. *Carpenter, P. H.* 1884,-88. (Report on the Crinoidea, etc.) *Challenger* Report, Zoology, vol. xi., No. 26, and vol. xxvi., No. 60. (With Bibliography of Recent Crinoids. The first volume contains much on Crinoids generally.)

21. —— 1891. (On certain points in the Morphology of the Cystidea.) Journ. Linn. Soc. London (Zool.), vol. xxiv. pp. 1-52, pl. i.

22. *Carpenter, P. H.* 1891. Geol. Mag., n.s., dec. iii., vol. viii. pp. 573-575. (Obituary notice, with supplementary Bibliography.)

23. *Carpenter, W. B.* 1866-76. (Structure, physiology, and development of *Antedon rosaceus.*) Phil. Trans. R. Soc. 1866, pp. 671-756, pls. xxxi.-xliii.; and Proc. R. Soc. vol. xxiv. pp. 211-231, pls. viii., ix. (Part 1 contains a valuable Historical Summary.)

24. —— 1884. (On the nervous system of the Crinoidea.) Proc. R. Soc., No. 232, pp. 67-76.

25. *Cumberland, G.* 1826. Reliquiae Conservatae, etc., 4to, x. and 45 pp., xiii. pls., Bristol. (Blastoids and Crinoids.)

26. *Danielssen, D. C.* 1892. (Crinoida) Norske Nordhavs-Exped. Zoologi, Part xxi., 28 pp., v. pls., 1 map, Christiania. (*Bathycrinus.*)

27. *Dujardin, F. and Hupé, H.* 1862. Histoire Naturelle des Zoophytes Echinodermes, etc., 8vo, 627 pp., x. pls., in Suites à Buffon, Paris. (A convenient summary to date.)

28. *Eichwald, E. v.* 1859. Lethaea Rossica . . . Ancienne Période, Livr. v. (Palaeozoic Crinoids and Cystids.)

29. *Etheridge, R., fil.* 1892. (Monograph of the Carboniferous and Permo-Carboniferous Invertebrata of New South Wales, II. Echinodermata, etc.) Mem. Geol. Surv. N.S.W., Pal., No. 5. (Crinoids.)

30. —— 1892. Chapters xxii., xxxii., xxxiv., and xxxix. in Jack and Etheridge, "The Geology and Palaeontology of Queensland and New Guinea," 8vo, Brisbane. (Crinoids, Blastoids, and Echinoids.)

31. —— *and Carpenter, P. H.* 1886. Catalogue of the Blastoidea in the . . . British Museum, 4to, xvi. + 322 pp., xx. pls., London.

32. *Follmann, O.* 1887. (Unterdevonische Crinoiden.) Verhandl. naturhist. Ver. preuss. Rheinl. Jahrg. xliv. pp. 113-138, pls. ii., iii.

33. *Forbes, E.* 1848. (On the Cystideae of the Silurian rocks of the British Islands.) Mem. Geol. Surv. Great Brit. vol. ii., part 2, pp. 483-538, pls. xi.-xxiii.

34. *Goldfuss, G. A.* 1826-1833. Petrefacta Germaniae, etc., Erster Theil, fol. x. and 252 pp. frontisp. and lxxii. pls., of which xl.-xliii. are double. (Div. II., Radiariorum Reliqq. pp. 115-214, pls. xxxix.-lxiv.)

35. *Gyllenhahl, J. A.* 1772. (Beskrifning på de så kallade Crystall-äplen ock kalk-bollar, såsom petreficerade Djur af Echini genus, eller dess närmaste slägtingar.) K. Svenska Vetenskaps-Acad. Handl. vol. xxxiii. pp. 239-261, pls. viii. and ix. (*Sphaeronis* and *Echinosphaera.*)

36. *Haeckel, E.* 1896. (Die Amphorideen und Cystoideen, etc.) Festschr. für Gegenbaur, No. 1, 179 pp., v. pls. (Bibliography.)

37. *Hall, J.* 1847, 1852, 1859. Palaeontology of New York, vols. i., ii., iii. in Natural History of New York, 4to, Albany. (Palaeozoic Crinoids and Cystids.)

38. —— 1848 onwards. (Annual Reports of the State Geologist.) Regents' Reports on State Cab. Nat. Hist. N.Y., 8vo, Albany. (Palaeozoic Pelmatozoa of all classes.)

39. —— 1858. Report on the Geological Survey of the State of Iowa, vol. i., Part ii., Palaeontology. (Palaeozoic Crinoids, Cystids, and an Edrioasteroid.)

40. *Hinde, G. J.* 1885. (New species of Crinoids with articulating spines.) Ann. Mag. Nat. Hist. (5), vol. xv. pp. 157-173, pl. vi. (*Hystricrinus,* = *Arthracantha.*)

41. *Hisinger, W.* 1837, 1840, 1841. Lethaea suecica, 124 pp., pls. A, B, C, i.-xxxvi. Supplementum secundum, 11 pp., pls. xxxviii. - xxxix. Supplementi secundi continuatio, 6 pp., pls. xl.-xlii., 4to. Holmiae.

42. *Jaekel, O.* 1891. (Ueber Holopocriniden [=Eugeniacrinidae and Holopodidae.]) Zeitschr. deutsch. geol. Ges., vol. xliii. pp. 557-671, pls. xxxiv.-xliii.

43. —— 1893. (Ueber Plicatocriniden, Hyocrinus, und Saccocoma.) Zeitschr. deutsch. geol. Ges., vol. xliv. pp. 619-696, pls. xxv.-xxx.

44. —— 1894. (Entwurf einer Morphogenie und Phylogenie der Crinoiden.) Sitzber. Ges. naturf. Freunde Berlin, Jahrg. 1894, pp. 101-121.

45. —— 1895. (Beiträge zur Kenntniss der paläozoischen Crinoiden Deutschlands.) Palaeont. Abhandl. Jena, neue Folge, vol. iii., 116 pp., x. pls.

46. —— 1895. (Organisation der Cystoideen.) Verhdl. deutsch. Zool. Ges., 1895, pp. 109-121. Prelim. to Stammesgeschichte der Pelmatozoen, I. 1899.

47. *Koenen, A. v.* 1886. (Neue Cystideen aus den Caradoc-schichten der Gegend von Montpellier.) Neues Jahrb. f. Min., 1886, II. pp. 246-254, pls. viii., ix.

48. —— 1887. (Beitrag zur Kenntniss der Crinoiden des Muschelkalks.) Abhandl. K. Ges. Wiss. Göttingen, vol. xxxiv., Phys. Kl. pp. 1-44, pl. i.

49. —— 1895. (Ueber die Entwickelung von *Dadocrinus gracilis* und *Holocrinus Wagneri*, etc.) Nachr. K. Ges. Wiss. Göttingen, Math.-Phys. Kl., 1895, pp. 283-293.

50. *Koninck, L. G. de, and Le Hon, H.* 1854. (Recherches sur les Crinoïdes du terrain Carbonifère de la Belgique.) Mém. Acad. Roy. Belgique, vol. xxvii., Mém. 3, 215 pp., vii. pls. (Crinoids and Blastoids. With very full Bibliography.)

51. *Loriol* (afterwards *Loriol le Fort*), *P. de.* 1877,-79. (Monographie des Crinoïdes Fossiles de la Suisse.) Mém. Soc. Pal. Suisse, vols. iv.-vi.

52. —— 1882-89. Paléontologie Française, 1re serie . . . Invertébrés. Terrain Jurassique. Tome XI., 1re partie, Crinoïdes, 8vo, Paris.

53. *Ludwig, H.* 1877. (Beiträge zur Anatomie der Crinoideen.) Zeitschr. wiss. Zool. vol. xxviii. pp. 255-353, pls. xii.-xix.

54. —— 1877. (Zur Anatomie des *Rhizocrinus lofotensis.*) *Op. cit.* vol. xxix. pp. 47-76, pls. v., vi.

55. *Marshall, A. M.* 1884. (On the nervous system of *Antedon rosaceus.*) Quart. Journ. Micr. Sci., n.s., vol. xxiv. pp. 507-548, pl. xxxv.

56. *Meek, F. B. and Worthen, A. H.* 1869. (Notes on some points in the structure and habits of the Palaeozoic Crinoidea.) Proc. Acad. Nat. Sci. Philadelphia, for 1868, pp. 323-334 ; reprinted in Amer. Journ. Sci. (2), vol. xlviii. pp. 23-40, and in Canad. Naturalist, n.s., vol. iv. pp. 434-452.

56*a*. —— See *Worthen, A. H.*, and others.

57. *Meyer, H. v.* 1826. (Beschreibung des Echino-Encrinites Senkenbergii, einer neu enddeckten Versteinerung.) Kastner's Archiv f. d. gesammte Naturlehre, vol. vii. pp. 185-192, pl. ii. (Nachtrag), *op. cit.* vol. viii. pp. 232-237.

58. —— 1837. (*Isocrinus* and *Chelocrinus.*) Mus. Senkenberg. vol. ii. pp. 251-263, pl. xvi.

59. *Miller, J. S.* 1821. A Natural History of the Crinoidea, etc., 4to, viii. +150 pp., l. pls., Bristol.

60. *Miller, S. A.* 1889,-92,-97. North American Geology and Palaeontology, etc., with two Appendices, 8vo, 793 pp., Cincinnati. (Index to first

descriptions of all N. American fossil Echinoderms; including references to Miller's numerous papers in Journ. Cincinnati Soc. Nat. Hist., and in the publications of the Illinois, Indiana, and Missouri Geol. Surveys.)

61. *Müller, Joh.* 1843. (Ueber den Bau des *Pentacrinus caput Medusae.*) Abhandl. Akad. Wiss. Berlin, Phys. Kl. vol. for 1841, pp. 177-248, vi. pls.

62. —— 1857. (Ueber neue Echinodermen des Eifeler Kalkes.) Abhandl. Akad. Wiss. Berlin, Phys. Kl. vol. for 1856, pp. 243-268, pls. i.-iv. (Crinoids.)

63. *Murchison, R. I.* 1839. The Silurian System, etc., 4to, xxxii. and 768 pp. London. (Crinoidea, by *J. Phillips.*)

64. *Neumayr, M.* 1889. Die Stämme des Thierreiches, vol. i. (all published), 8vo, vi. + 603 pp., Vienna. (Phylogeny of all Echinoderms.)

65. *Oehlert, D. P.* 1879. (Deux nouveaux genres de Crinoïdes du terrain dévonien de la Mayenne.) Bull. Soc. géol. France (3), vol. vii. pp. 6-10, pls. i., ii. (*Thylacocrinus.*)

66. —— 1882. (Crinoïdes nouveaux du Dévonien, etc.) *Ser. cit.* vol. x. pp. 352-363, pls. viii., ix.

67. —— 1891. (*Spyridiocrinus*), *ser. cit.* vol. xix. pp. 220-227, pls. vii., viii.

68. —— 1892. (Deux Crinoïdes nouveaux du Dévonien), *tom. cit.* pp. 834-853, pl. xviii. (*Diamenocrinus.*)

69. —— 1896. (Fossiles dévoniens de Sta. Lucia), *ser. cit.* vol. xxiv. pp. 814-875, pls. xxvi.-xxviii. (Crinoids and Blastoids.)

70. *Orbigny, A. D. de.* 1840,-58. Histoire naturelle . . . des Crinoïdes, etc., 4to, 98 pp., xviii. pls., Paris. (Apiocrinidae, Bourgueticrinidae.)

71. —— 1849-52. Cours élémentaire de Paléontologie, etc., 2 vols. and Atlas. Prodrome de Paléontologie . . . des animaux mollusques et rayonnés. 3 vols., Paris.

72. *Perrier, J. O. E.* 1886,-90. (Mémoire sur l'organisation et le développement de la Comatule de la Méditerranée.) Nouv. Arch. Mus. Hist. Nat. (2), vol. ix. pp. 53-348, x. pls., and (3), vol. i. pp. 169-286, vol. ii. pp. 1-86, pls. i., ii.

73. *Pictet, F. J.* 1857. Traité de Paléontologie, 2^{e} édit. vol. iv. Crinoïdes (Blastoïdes et Cystidées), pp. 278-345, Paris.

74. *Pompeckj, J. F.* 1896. (Die Fauna des Cambrium von Tejřovic und Skrej in Böhmen.) Jahrb. geol. Reichsanst. Wien, vol. xlv. pp. 495-614, pls. xiii.-xvii. (Cystidea and Edrioasteroidea.)

75. *Quenstedt, F. A.* 1874-76. Die Asteriden und Encriniden nebst Cysti- und Blastoideen, Petrefactenkunde Deutschlands, 1 Abth. vol. iv., 8vo, viii. and 742 pp., Atlas pls. xc.-cxiv., Leipzig.

76. —— 1885. Handbuch der Petrefactenkunde, Dritte Auflage, 4 Abth. pp. 801-988, pls. lxiii.-lxxx., Tübingen.

77. *Roemer, C. F.* 1851. (Monographie der . . . Blastoideen, etc.) Arch. Naturges. vol. xvii. (1), pp. 323-352, pls. iv.-viii.

78. —— 1855. (Crinoidea, etc.) Lethaea Geognostica, 3rd ed., vol. ii. pp. 210-280, Stuttgart. (All Palaeozoic Pelmatozoa.)

79. *Rouault, M.* 1883. Œuvres posthumes. Amorphozoaires siluriens, publiées par Lebesconte, 4to, 73 pp., xxii. pls., Rennes. (Amphoridea.)

80. *Salter, J. W., and Billings, E.* 1858. (On *Cyclocystoïdes*, etc.) Canad. org. Remains, dec. iii., pp. 86-90, pl. x. bis.

81. *Sars, M.* 1868. Mémoires pour servir à la connaissance des Crinoïdes vivants, 4to, 65 pp., vi. pls., Christiania. (*Rhizocrinus, Antedon.*)

82. *Schmidt, F. B. von.* 1874. (Miscellanea Silurica, II. Ueber einige neue und wenig bekannte Baltisch-Silurische Petrefacten.) Mém. Acad. Imp. Sci. St-Pétersbourg (7), vol. xxi. pp. 1-48, pls. i.-iv.

83. —— 1880. (Ueber *Cyathocystis Plautinae*, etc.) Verhandl. Mineral. Ges. St. Petersburg (2), vol. xv. pp. 1-7.

84. *Schultze, L.* 1867. (Monographie der Echinodermen des Eifler Kalkes.) Denkschr. Akad. Wiss. Wien, Math.-nat. Kl. vol. xxvi. pp. 113-230, pls. i.-xiii.

85. *Shumard, B. F.* 1866. (A Catalogue of the Palaeozoic Fossils of N. America.) Trans. Acad. Sci. St. Louis, vol. ii. pp. 334-407. (Contains also "A Chronological List of Works which contain Descriptions or Notices of N. American Palaeozoic Echinodermata" from 1811 to 1865.)

86. *Trautschold, H.* 1879. (Die Kalkbrüche von Mjatschkowa . . . Schluss.) Nouv. Mém. Soc. Nat. Moscou, vol. xiv. pp. 101-180, pls. xii.-xviii. (Carboniferous Crinoidea.)

87. *Volborth, A. v.* 1842. (Ueber der Echinoencrinen.) Bull. Scient. Acad Imp. Sci. St-Pétersbourg, vol. x. pp. 293-303, pls. i. and ii.

88. —— 1844. (Ueber die Arme der bisher zu dem armlosen Crinoiden gezählten Echino-Encrinen.) Bull. Classe Phys.-Math. Acad. Imp. Sci. St-Pétersbourg, vol. iii. No. 6, columns 91-96, with 1 plate.

89. —— 1846. (Ueber die russischen Sphaeroniten, eingeleitet durch einige Betrachtungen ueber die Arme der Cystideen.) Verhandl. Mineral. Ges. St. Petersburg, 1845-46, pp. 161-198, pls. ix., x.

90. —— 1870. (Ueber *Achradocystites* und *Cystoblastus* . . . eingeleitet durch kritische Betrachtungen ueber die Organe des Cystideen.) Mém. Acad. Sci. St-Pétersbourg (7), vol. xvi., No. 2, 15 pp.

91. *Wachsmuth, C., and Springer, F.* 1879-1886. (Revision of the Palaeocrinoidea.) Proc. Acad. Nat. Sci. Philadelphia, for 1879, pp. 226-378, pls. xv.-xvii.; for 1881, pp. 177-411, pls. xvii.-xix.; for 1885, pp. 225-364, pls. iv.-ix.; for 1886, pp. 64-226. (Index to all genera and species of Palaeozoic Crinoids, with references to literature.)

92. —— 1897. (North American Crinoidea Camerata.) Mem. Mus. Harvard, vol. xx. and xxi. (Contains also chapters on morphology and classification of Crinoids in general.) For other writings see under 10.

93. *Woodward, H.* 1880. (Notes on the Anomalocystidae, etc.) Geol. Mag., n.s., dec. ii., vol. vii. pp. 193-201, pl. vi.

94. *Worthen, A. H.*, with *Meek, F. B.; Miller, S. A.; Wachsmuth, C.; Barris, W. H.; Springer, F.*, and others. 1866-90. Palaeontology of Illinois, in Geol. Survey Illinois, vols. ii., iii., v., vi., vii., and viii. (Palaeozoic Echinoderma, especially Pelmatozoa, with references to the numerous preliminary papers in Proc. Acad. Nat. Sci. Philadelphia. Vol. viii. contains complete Index and a Bibliography of A. H. Worthen, both by *J. Lindahl.*)

95. *Zittel, K. A. v.* 1879. Handbuch der Palaeontologie, I. Band. Palaeozoologie, I. Band, 1 Abth., pp. 308-560, München. (All fossil Echinoderma.)

96. —— 1895. Grundzüge der Palaeontologie (Palaeozoologie), 8vo, viii. and 971 pp., München. First portion translated as "Text-Book of Palaeontology," by *C. R. Eastman*, 1896, with revision for Pelmatozoa by *C. Wachsmuth* and others, 8vo, New York. Reïssue, 1900, London.

See also Nos. 5, 21, and 36 in Literature of Echinoderma generally (p. 35).

CHAPTER XIII.

ELEUTHEROZOA—THE HOLOTHURIOIDEA.

GRADE B. ELEUTHEROZOA.

CLASS I. HOLOTHURIOIDEA.
" II. STELLEROIDEA.
" III. ECHINOIDEA.

ECHINODERMA in which the theca, which may be but slightly or not at all calcified, is not attached by any portion of its surface, but is usually placed with the oral surface downwards or in the direction of forward locomotion. Food is not conveyed by a subvective system of ciliated grooves, but is taken in directly by the mouth. The anus when present is typically aboral and approaches the mouth only in a few specialised forms. The aboral nervous system, if indeed it be present at all, is very slightly developed. The circumoesophageal water-ring may lose its connection with the exterior medium; the podia (absent only in some exceptional forms) may be locomotor, respiratory, or sensory in function, but usually are locomotor tube-feet.

As explained on p. 33, the genetic affinity between the three classes now to be dealt with is not so obvious as that between the classes of Pelmatozoa. Some writers have taken the Holothurioidea to be the most primitive class of Echinoderms, or at least to be widely separated from the Stelleroidea and Echinoidea. Without denying a large measure of truth to such statements, it is here maintained that all these three classes bear the impress of a Pelmatozoic ancestry. And, though they arose from the Pelmatozoan stem, probably at different periods, and possibly from different branches thereof, yet the trend of the evolution of each was in the same direction—a direction opposed to that of the Pelmatozoa.

At any rate the plain facts set down in the above definition are conveniently connoted and emphasised by the adoption of the term Eleutherozoa, whatever be the precise systematic value attached to it. In discussing the Eleutherozoan classes, the order followed is from the more primitive to the more specialised.

CLASS I. HOLOTHURIOIDEA, C. T. v. Siebold (1848)[1]

(= Fistulides, Lamarck, 1801; Scytodermata, Burmeister, 1837; Ascidiastella, T. & T. Austin, 1840; Scytactinota, Bronn, 1860).

Order 1. **Actinopoda.**
,, 2. **Paractinopoda.**

Eleutherozoic Echinoderms normally elongate along the oro-anal axis, which axis and the dorsal hydropore lie in the sagittal plane of a secondary bilateral symmetry. The calcareous skeleton, which may be entirely absent, is usually in the form of minute spicules, sometimes of small irregular plates with no trace of a calycinal or apical system; to these is added a ring of pieces radiately arranged round the oesophagus. Ambulacral appendages take the form of: (1) circumoral tentacles, (2) sucking-feet, (3) papillae; of these (1) alone is always present. The gonads are not radiately disposed.

The Holothurians have long been known to man. Many of the common forms are large and conspicuous animals, which are frequently caught in the dredge or thrown up on our shores. It is generally supposed that these are the marine animals to which Aristotle gave the name of ὁλοθούριον, from which their present scientific name has been derived. Pliny, mentioning a species of *Cucumaria*, calls it *Cucumis marinus*, or sea-cucumber, a name often applied to Holothurians at the present day.

Belon, in 1553, first described a Holothurian, recognising some of its affinities to the starfish and sea-urchins; and Rondelet, two years later, gave some figures of two species. Bohadsch, Pallas, Fabricius, Cuvier, and others increased our systematic and anatomical knowledge of this group during the later part of the eighteenth century. In 1816 Tiedemann published an excellent account of the anatomy of *Holothuria tubulosa*, Gmel. (12), and since then the study of the structure, development, and classification of the class has been greatly extended by a large number of naturalists, amongst whom one may mention A. Baur (1), Selenka (7), Semper (10), Joh. Müller, Metschnikoff, and Kowalevsky. Within recent years the finer anatomy and histology of Holothurians have been studied by O. Hamann (3), Hérouard (4), Cuénot, and many others, and their embryology by Selenka (7), Semon (9), and Bury (2). Our knowledge of that most interesting group, the Elpidiidae, dates almost entirely from the publication by Théel of the Report on the collections made during the Challenger Expedition (11). The family Pelagothuriidae has only lately been described by H. Ludwig (6). An admirable and comprehensive treatise on the

---

[1] By E. S. Goodrich, M.A.

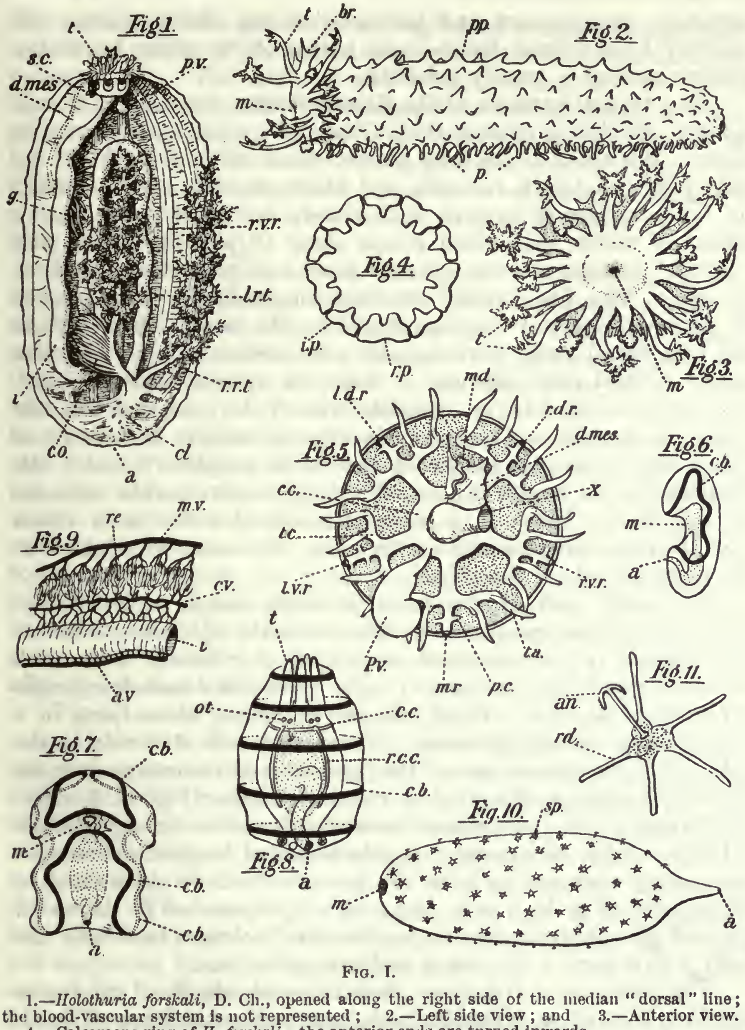


Fig.1.
t
s.c.
d.mes
p.v.
g.
r.v.r.
l.r.t.
r.r.t
i
c.o.
a
cl
Fig.2.
t
br.
pp
m
p.
Fig.3.
t
m
Fig.4.
i.p.
r.p.
Fig.5.
md.
l.d.r
r.d.r.
d.mes.
c.c.
x
t.c.
l.v.r
r.v.r.
Pv.
m.r
p.c.
t.a.
Fig.6.
c.b.
m
a
Fig.9.
re
m.v.
c.v.
i
a.v
Fig.7.
c.b.
m
c.b.
c.b.
a.
Fig.8.
t
ot
c.c.
r.c.c.
c.b.
a
Fig.11.
an.
rd.
Fig.10.
sp.
m
a

Fig. I.

1.—*Holothuria forskali*, D. Ch., opened along the right side of the median "dorsal" line; the blood-vascular system is not represented; 2.—Left side view; and 3.—Anterior view.
4.—Calcareous ring of *H. forskali;* the anterior ends are turned inwards.
5.—Diagram of the water-vascular system of *H. forskali*, illustrating the Actinopod plan.
6.—Larva of a Holothurian. (After Balfour.) 7.—*Auricularia* larva; and 8.—Barrel-shaped larva of *Synapta digitata*. (Both after Semon; cf. Chapter VIII., Figs. III. & XVII.)
9.—Portion of the intestine with the accompanying blood-vessels and rete mirabile of *Holothuria tubulosa*. (After Tiedemann.)
10.—Left side view of *Ankyroderma affine*, Dan. and Kor.; and
11.—Spicules of the same. (After Danielssen and Koren.)
a, anus; *an*, anchor; *a.v*, anti-mesenterial blood-vessel; *br*, brim; *c.b*, ciliated band; *c.c*, circular water-vascular canal; *cl*, rectal "cloaca"; *c.o*, Cuvierian organs; *c.v*, collateral blood-vessel; *d.mes*, dorsal mesentery; *g*, gonad; *i*, intestine; *i.p*, interradial piece; *l.d.r*, left dorsal radius; *l.v.r*, left ventral radius; *l.r.t*, left respiratory tree; *m*, mouth; *md*, madreporite; *m.r*, median ventral radius; *m.v*, mesenterial blood-vessel; *ot*, otocyst; *p*, podium; *p.c*, podial canal; *pp*, papilla; *p.v*, Polian vesicle; *r.cc*, radial canal; *rd*, spatulate rod; *r.d.r*, right dorsal radius; *re*, rete mirabile; *r.p*, radial piece; *r.r.t*, right respiratory tree; *r.v.r*, right ventral radius; *s.c*, stone-canal; *sp*, spicules; *t*, tentacle; *t.a*, tentacle ampulla; *t.c*, tentacle canal; *x*, oesophagus.

structure, development, and taxonomy of the Holothurioidea has recently been written by the same author (5), to whose works the present account is greatly indebted.

As a **typical example of the Holothurioidea** the common Cotton spinner, *Holothuria forskali*, Delle Chiaje (*H. nigra*, auctt.), may be taken. It is about 20 cm. long, almost cylindrical in shape (Fig. I. 2), pale yellowish-brown beneath, and black above. The "ventral" or lower surface is covered with closely set retractile podia, by means of which the animal creeps along (2, *p*); the lateral and "dorsal" surfaces are covered with small and large conical papillae (2, *pp*). The five "radii" running longitudinally from mouth to anus are scarcely distinguishable on the outer surface; there are two dorsal radii (bivium), and one median ventral, and two lateral ventral radii (trivium). Near the anterior end the body-wall is produced into an irregular brim (2, *br*); beyond this the animal terminates in a smooth pale-coloured area, in the centre of which lies the mouth, somewhat ventral in position (2 and 3, *m*). Surrounding the mouth is a set of twenty semi-retractile tentacles (2 and 3, *t*). When in a state of contraction the brim closes over the retracted tentacles and mouth. The anus is situated at the posterior pole of the animal.

The body-wall of *Holothuria* is thick, tough, and leathery. Externally a thin transparent cuticle covers the epidermis, which is not ciliated, and is composed of a layer of columnar cells, with scattered gland cells and sensory cells. The thick underlying cutis is formed of connective tissue cells and numerous fibres lying in a homogeneous ground substance. Wandering cells are found in the cutis, while the greater part of the pigment is in its outermost layer. Below the cutis is the layer of circular muscles (Fig. II. 5, *c.m*)[1] interrupted at the radii, except immediately round the anus, where it forms a sphincter muscle. A paired band of longitudinal muscles runs along each radius from the posterior end of the animal to the anterior (Fig. II. 1 & 5, *l.m*); here it is attached to the radial plate of the calcareous ring to be described below. Internally the body-wall is lined with ciliated coelomic epithelium.

The skeleton of *Holothuria forskali* consists chiefly of calcareous spicules, knotted or branching rods, and perforated discs (Fig. II. 6, *A*, *B*), secreted by connective tissue cells and forming a thin layer in the outer region of the cutis, especially on the papillae and ambulacral appendages (podia and tentacles). Spicules may also be found in the connective tissue throughout the body, and they are very numerous in the wall of the stone-canal and madreporite. A large perforated plate is situated at the extremity of each podium. A ring of ten calcareous pieces surrounds the oesophagus; the five radial pieces are notched and larger than the interradial (Fig. I. 4).

---

[1] This figure refers to the allied species *Holothuria tubulosa*, Gmelin.

The nervous system consists of a "superficial" ring surrounding the mouth and giving off five radial nerves which run backwards to the posterior end. The tentacles and viscera are supplied by nerves from the ring; the podia by branches from the radial nerves. The ring and the radial nerves are sunk below the surface, and lie on the inner side of the cutis. An epineural canal lies outside the radial nerves. Following each radial nerve on its inner surface is a small "deep" nerve, from which are supplied the muscles of the body-wall (Fig. II. 4).

The water-vascular system consists of a circular canal surrounding the oesophagus behind the calcareous ring, and giving off five radial canals (Fig. II. 5, *c.c* and *r.c*). Each radial canal passes forward between the calcareous ring and oesophagus, and then outwards, through the notch in the radial piece, to the body-wall; it then runs backwards below the radial nerve. The radial canals send off a branch on either side to supply a pair of tentacles, each tentacle being provided with a long ampulla freely projecting into the body-cavity (Fig. I. 5, *t.a*, and Fig. II. 5). A Polian vesicle is attached to the circular canal in the left ventral interradius. Branches are given off from the radial canals in the body-wall to supply the podia and papillae; small ampullae are here present. A twisted stone-canal lying in the median dorsal line leads from the circular canal to a madreporite, pierced with many small apertures, and lying in the body-cavity at the anterior edge of the dorsal mesentery (Fig. I. 1 and 5, *s.c* and *md*).

The alimentary canal is looped (Fig. I. 1, *i*, and Fig. II. 1), coiled in the direction of the watch-hand as viewed from the anterior end, and supported almost throughout by a mesentery attached to the body-wall. The mouth leads into a wide oesophagus, which narrows on passing backwards out of the calcareous ring. A scarcely distinguishable stomach succeeds the oesophagus and passes into the long intestine, which finally ends in a rectal "cloaca" opening at the anus. The oesophagus, stomach, and part of the intestine form the first region of the alimentary canal, running backwards and supported by the median dorsal mesentery. Near the hinder end of the body the intestine and mesentery cross over from the dorsal interradius to the left lateral dorsal interradius, up which they run. Near the anterior end this second section of the intestine, with its mesentery, crosses to the right ventral interradius, down which the third and last portion of the intestine runs straight to the anus. Round the oesophagus, bounded externally by the calcareous ring and the radial canals, a portion of the coelom is incompletely shut off from the general body-cavity (Fig. II. 5, *pr*); connective tissue strands run across it from one wall to the other. The enlarged rectum, or cloaca, is fastened on all sides to the body-wall by muscular strands (Fig. I. 1, *cl*).

Opening into the anterior and dorsal region of the cloaca by a common duct are the respiratory trees, two large tubes which give off numerous side-branches ending blindly in tufts of slender twigs (Fig. I. 1, *l.r.t* and *r.r.t*). Coming off from the base of the

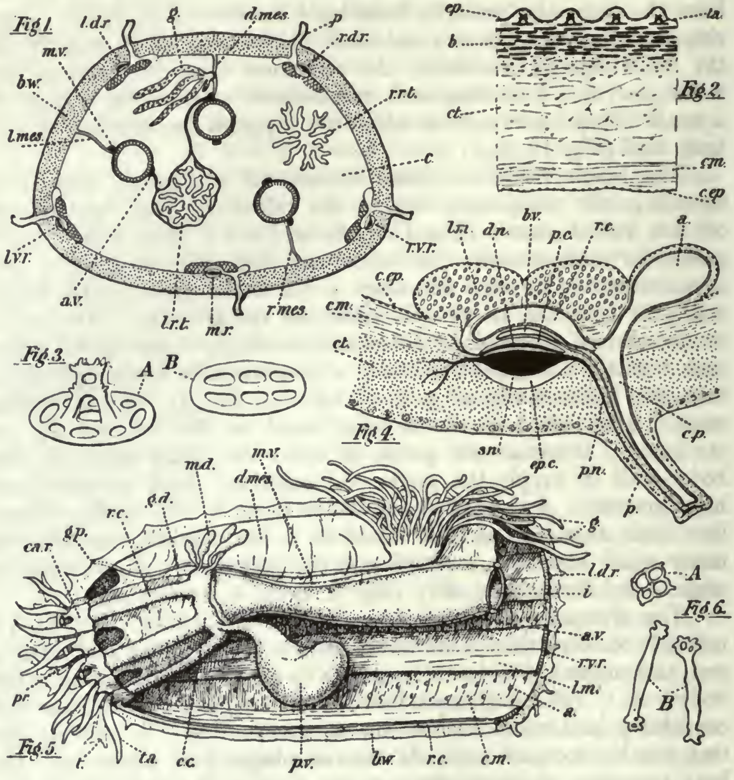


Fig.1.
l.dr
g.
d.mes.
p
r.d.r.
m.v.
b.w.
r.r.t.
l.mes.
c.
l.v.r.
r.v.r.
a.v.
l.r.t.
m.r.
r.mes.
Fig.2.
ep.
ta.
b.
ct.
c.m.
c.ep
Fig.3.
A
B
l.m.
d.n.
b.v.
p.c.
r.c.
a.
c.ep.
c.m.
ct.
Fig.4.
s.n.
ep.c.
p.n.
c.p.
p.
m.v.
md.
d.mes.
g.d.
r.c.
g.p.
ca.r.
g.
l.d.r.
i
a.v.
r.v.r.
l.m.
a.
pr.
Fig.5.
t.
t.a.
c.c.
p.v.
b.w.
r.c.
c.m.
A
Fig.6.
B

Fig. II.

1.—Transverse section of one of the Holothurinae. (Modified from Ludwig and Lang.)
2.—Transverse section of the body-wall of *Holothuria impatiens*, Forskål.
3.—(*A*) "table" and (*B*) "biscuit" spicule of the same.
4.—Transverse section of the radius of an Actinopod Holothurian. (After Lang.)
5.—Left side view of the anterior region of *Holothuria tubulosa*, Gmel., from which the left side of the body-wall has been removed.
6.—(*A*) perforated disc, and (*B*) branching rod spicule of *Holothuria forskali*.

a, ampulla ; *a.v*, anti-mesenterial blood-vessel ; *b*, "biscuit" spicule ; *b.v*, blood-vessel ; *b.w*, body-wall ; *c*, coelom ; *car*, calcareous ring ; *c.c*, circular canal ; *c.ep*, coelomic epithelium ; *c.m*, circular muscles ; *c.p*, podial canal ; *ct*, cutis ; *d.mes*, dorsal mesentery ; *d.n*, deep nerve ; *ep*, epidermis ; *ep.c*, epineural canal ; *g*, gonad ; *g.d*, genital duct ; *g.p*, genital pore ; *i*, intestine ; *l.d.r*, left dorsal radius ; *l.m*, longitudinal muscles ; *l.mes*, left mesenterial ; *l.r.t*, left respiratory tree ; *l.v.r*, left ventral radius ; *md*, madreporite ; *m.r*, median ventral radius ; *m.v*, mesenterial blood-vessel ; *p*, podium ; *p.c*, pseudhaemal canal ; *p.n*, podial nerve ; *pr*, peripharyngeal coelom ; *p.v*, polian vesicle ; *r.c*, radial canal ; *r.d.r*, right dorsal radius ; *r.mes*, right mesenterial fold ; *r.r.t*, right respiratory tree ; *r.v.r*, right ventral radius ; *s.n*, superficial nerve; *t*, tentacle ; *t.a*, tentacle ampulla ; *ta*, "table" spicule in 2.

left respiratory tree are a large number of long slender processes, the Cuvierian organs (Fig. I. 1, *c.o*). These remarkable organs, formed of spirally coiled fibrous tissue covered with a layer of modified coelomic epithelium which secretes a sticky substance, are shot out of the anus through the wall of the cloaca by the living animal when irritated. The organs swiftly elongate, forming adhesive white threads, to which this Holothurian owes its name of Cotton-spinner.

The blood-vascular system consists of a circular vessel round the oesophagus, giving off five radial vessels which run between the water-vascular canal and the pseudhaemal canal, covering the radial nerve internally. The anterior region and genital organs are supplied from the circular vessel. The alimentary canal is provided with two longitudinal trunks coming from the circular vessel—one, the "dorsal" or mesenterial vessel, runs along the region where the mesentery is attached to the intestine; the other, the "ventral" or antimesenterial, runs along the alimentary canal on the opposite side (Fig. II. 1 and 5, *m.v* and *a.v*). A cross vessel passes from the mesenterial vessel on the first region of the intestine to the antimesenterial vessel on the second region. In connection with the mesenterial vessel (especially along the second region of the intestine) is an extensive and rich plexus of blood-vessels, the rete mirabile, overlying the left respiratory tree (Fig. I. 9). Blood lacunae extend in the walls of the alimentary canal, respiratory trees, gonads, and other parts.

A closed pseudhaemal system extends over the inner surface of the nerve ring and radial nerves.

The body-cavity forms a continuous coelomic space lined throughout by epithelium, which is generally ciliated.

The sexes are separate in this species. The genital organs consist of a bunch of tubes, with free blind ends lying in the coelom, and uniting at their base to open into a duct running forwards in the dorsal mesentery (Fig. II. 1 and 5, *g* and *g.d*). The genital duct opens by a median dorsal pore behind the tentacles (5, *g.p*).

Variation in the Holothurioidea.—In outward form the more specialised and highly modified genera depart very widely from the elongated and somewhat pentagonal shape which appears to be the more primitive. In organisation, however, this group is fairly constant, and clearly defined from the other classes of Echinoderma. The epidermis is not ciliated in the adult. The body-wall is remarkable for its thickness and leathery consistency, the calcareous skeleton being rarely in the form of plates or scales, and more often as minute spicules of various shapes (there is no apical system of plates). When these spicules are of different kinds they generally form distinct layers in the cutis—as, for instance, in *Holothuria impatiens*, where the "tables" lie on the surface, whilst the "biscuit" spicules are disposed in a thick inner layer (Fig. II. 2 and 3, *ta*, *b*). The spicules are deposited by cells in the cutis, and develop first as small rods which become branched at each end; by the increase of the number of branches and their repeated fusion arise the innumerable varieties of spicules found in different species of Holothurians. These calcareous bodies are of great value to the systematist in classifying the smaller groups, such as genera and species.[1] Although their general characteristics are fairly similar within the several families, the different shapes of spicules are not sufficiently constant to be used as diagnostic characters of such large divisions.

Very characteristic of the Holothurians is the calcareous ring formed of radial and interradial pieces surrounding the oesophagus. Occupying the same position as "Aristotle's lantern" in the Echinoids, it may possibly be homologous with that organ.

A well-developed muscular system is present in the body-wall, whereby the animal can move and alter its shape. The longitudinal muscles, generally paired radial bands, often form special retractors for the withdrawal of the anterior region of the body. In the Synaptidae alone the circular muscles are not interrupted at the radii.

Although the nervous and water-vascular systems are distinctly built according to the pentagonal radiate Echinoderm type, yet the latter system is generally modified in relation to the very frequent differentiation of a dorsal surface occupying the three upper interradii, and of a flattened ventral surface or creeping sole occupying the two lower interradii. The ambulacral appendages, the podia, may become modified from typical sucking-feet into pointed papillae. Either the tube-feet or the papillae may extend over the entire interradial space. On the other hand, both tube-feet and papillae may be absent (Molpadiidae, Pelagothuriidae, and Synaptidae), and even the radial canals may disappear in the adult (Synaptidae). The oral tentacles, so characteristic of the Holothurians, are no doubt modified ambulacral appendages homologous with the podia. They vary greatly in number and shape, and are of great taxonomic value, being almost invariably more or less peltate in the Holothuriidae and Elpidiidae, arborescent in the Cucumariidae, and digitate or pennate in the Molpadiidae and Synaptidae.

The Polian vesicle is usually single, and situated in the left ventral interradius; but there are sometimes more than one. The stone-canal, generally single, lies in the median dorsal mesentery. Although in some of the Holothuriidae, Elpidiidae, and Pelagothuriidae, and in the larvae of other forms, the stone-canal retains its opening to the exterior in the median dorsal line, in most Holothurians this condition is modified, in that the primitive madreporite disappears, the connection with the body-wall is lost, and the canal opens by a new madreporite into the body-cavity. In some species numerous accessory stone-canals and madreporites may be developed (Fig. II. 5, *md*).

---

[1] The structure of the spicules is liable to alter during the lifetime of the individual (Hérouard, Mitsukuri, Östergren).

The disposition of the organs in the radius, as seen in transverse section, is distinctive (Fig. II. 4). The superficial radial nerve is separated from the epidermis by the thick cutis and a space (epineural canal). The deep radial nerve is separated from the ambulacral radial canal by a pseudhaemal canal and the radial blood-vessel. Over all lies the longitudinal muscle internally. This arrangement resembles most that found in the Echinoidea.

The alimentary canal and the mesentery which supports it have the dextral coil characteristic of Echinoderma, as described above for *Holothuria* (p. 221).

The respiratory trees, organs quite peculiar to this class, are by no means of universal occurrence, being absent in the Elpidiidae, Pelagothuriidae, and Synaptidae. It is interesting to note, however, that in certain of the Elpidiidae the rectum is provided with a caecum, which may represent a vestige or a rudiment of the respiratory trees (Fig. III. 10, *coe*).

The Cuvierian organs (p. 223) appear to be modified branches of the respiratory trees.

The Holothurioidea are distinguished from the remainder of the Echinoderma by the structure of the genital organs. These always consist of a single, or of a right and left, tuft of tubules leading into a common duct, which runs in the dorsal mesentery and opens to the exterior in the median dorsal line near the anterior extremity of the body. There is no axial organ or sinus, and no trace of radial structure in connection with the gonads (see p. 24).

As a rule, the genital products are shed in the sea, where fertilisation and development take place. Rarely, as in *Chiridota rotifera* (Pourt.) and *Phyllophorus urna* (Grube), the young develop in the body-cavity of the parent. Brood chambers are formed in *Psolus ephippifer* (W. Thomson) and some species of *Cucumaria.*

A total and almost equal segmentation of the fertilised egg leads to the formation of a ciliated blastula and gastrula, from which is developed the characteristic *Auricularia* larva (Fig. I. 6, 7). The free-swimming *Auricularia* has an alimentary canal provided with a mouth and anus, and the cilia are restricted to a single large circumoral band and a small adoral band within the mouth. The archenteron now gives rise to the hydro-enterocoel, opening by the primary stone-canal at a pore a little to the left of the median dorsal line. Later the circumoral ciliated band becomes greatly folded, and then converted into the circular ciliated rings of the barrel-shaped larva or pupal stage (Fig. I. 8). The mouth shifts to the anterior pole, round which are developed the tentacles as the first appendages of the water-vascular system. The radial canals and podia (when present) are now formed, and the young Holothurian assumes the adult form. Rarely the *Auricularia* stage is omitted, the ciliated gastrula developing more or less directly into the barrel-shaped larva.

Very little is known of the extinct Holothurians. Some spicules have been found, many of which belong to the Synaptidae, in deposits ranging from the Carboniferous to Tertiary strata.

With advancing knowledge the **Classification** of the Holothurians has undergone many changes since it was first attempted at the beginning of this century. It now appears to be firmly established on deep-seated structural characters. In 1815 Oken divided the few species then known according to the shape of the body, whilst soon after Lamarck made use of the tentacles as a taxonomic character, a system afterwards perfected by Grube, who founded the family Aspidochirotae for forms with peltate tentacles (Holothuriidae), and Dendrochirotae for forms with arborescent tentacles (Cucumariidae). Cuvier and others followed Oken, taking into account the occurrence and distribution of the podia; and Brandt divided the *Holothuria* into Pedatae with podia, and Apodes without podia. Selenka, in 1867, following Jaeger, formed the two orders Pneumophora and Apneumona, the first for the modern Holothuriidae, Cucumariidae, and Molpadiidae, provided with respiratory trees or "lungs," the second for the Synaptidae without "lungs." Théel adopted the orders Apoda and Pedata, adding the order Elasipoda for the newly discovered Elpidiidae. Ludwig has clearly shown that the classifications founded on the mere presence or absence of podia or of respiratory trees are artificial; first, separating off the Synaptidae, which differ in important respects from all the other families, as the Paractinopoda, he divides the remainder of the Holothurians, the Actinopoda, into five families, as shown in the following table :—

Order 1. **Actinopoda.** Radial canals supplying tentacles and podia.	
A. With respiratory trees.	
(*a*) With podia.	Fam. 1. Holothuriidae. Fam. 4. Cucumariidae.
(*b*) Without podia	Fam. 5. Molpadiidae.
B. Without respiratory trees.	
(*a*) With podia.	Fam. 2. Elpidiidae.
(*b*) Without podia.	Fam. 3. Pelagothuriidae.
Order 2. **Paractinopoda.** Neither radial canals nor podia. Tentacles supplied from circular canal.	Fam. Synaptidae.

ORDER 1. **Actinopoda**, Ludwig.

The five radial canals of the water-vascular system, springing from the circular canal, supply the tentacles and podia (Fig. I. 5).

FAMILY 1. HOLOTHURIIDAE. Body more or less flattened ventrally to form a creeping sole. Mouth generally somewhat ventral in position. Spicules chiefly in the form of tables, rods, and perforated plates. Calcareous ring of five radial and five interradial pieces. Ambulacral appendages present in the shape of tube-feet, papillae, and peltate tentacles (generally twenty). Respiratory trees well developed. SUB-FAMILY 1. SYNALLACTINAE. No tentacular ampullae. Stone-canal single, and joined to the body-wall. No rete mirabile. Genera—A. With genital tubes in a right and left bundle—*Pseudostichopus*, Théel; *Paelopatides*, Théel; *Meseres*, Ludwig; *Synallactes*, Ludwig; *Bathyplotes*, Östergren. B. Genital tubes in a tuft on the left side only—*Mesothuria*, Ludwig. SUB-FAMILY 2. HOLOTHURIINAE. Well-developed tentacular ampullae. Stone-canals often numerous, and with complex madreporites not connected with the body-wall (exc. *Holothuria lactea*). The left respiratory tree is enveloped in a vascular network, the rete mirabile. Cuvier's organs often present. Genera—A. With genital tubes in a tuft on the left side only—*Muelleria*, Jäger, mostly tropical; *Labidodemas*, Selenka, tropical; *Holothuria*, Linn., to which genus belong the British Cotton-spinner described above (p. 220), and *H. edulis*, one of the kinds of edible Trepang. B. With genital tubes in a right and left tuft—*Stichopus*, Brandt.

The Holothuriidae are characterised not only by the possession of well-developed respiratory trees, and of from fifteen to thirty peltate tentacles (formed of a thick stem branching at its extremity), but also by the absence of retractor muscles, and of auditory vesicles. The tube-feet and papillae may be in double radial rows, as in *Labidodemas*, in several rows, as in *Stichopus*, or scattered, as in *Holothuria*. The calcareous ring is generally composed of short, compact pieces; it appears to be absent in *Paelopatides* and *Synallactes*. The anus in *Pseudostichopus* is situated in a deep vertical furrow, whilst in *Muelleria* it is surrounded by five pointed, calcareous plates. The longitudinal muscles are in paired bands, except in *Pseudostichopus*.

The Holothuriinae are a well-differentiated group distinguished by the possession of large tentacular ampullae projecting freely into the body-cavity (Fig. II. 5, *t.a*), internal madreporites (5, *md*), and a vascular plexus surrounding the left respiratory tree. The Synallactinae, on the other hand, are in many respects intermediate between the former sub-family and the Elpidiidae. The absence of tentacular ampullae, and of the rete mirabile, and the presence of a single stone-canal connected with the body-wall and probably retaining its primitive opening to the exterior, are all characters uniting the Synallactinae to the Elpidiidae, with which they have indeed been classified (Östergren).

FAMILY 2. ELPIDIIDAE. Body generally flattened ventrally. Mouth more or less ventral. Tentacles, ten to twenty, more or less peltate. Ventral tube-feet and dorsal papillae present (exc. *Capheira*). Often auditory vesicles on the radial nerves. Stone-canal single; madreporite frequently opening to the exterior. Respiratory trees absent (or rudimentary).

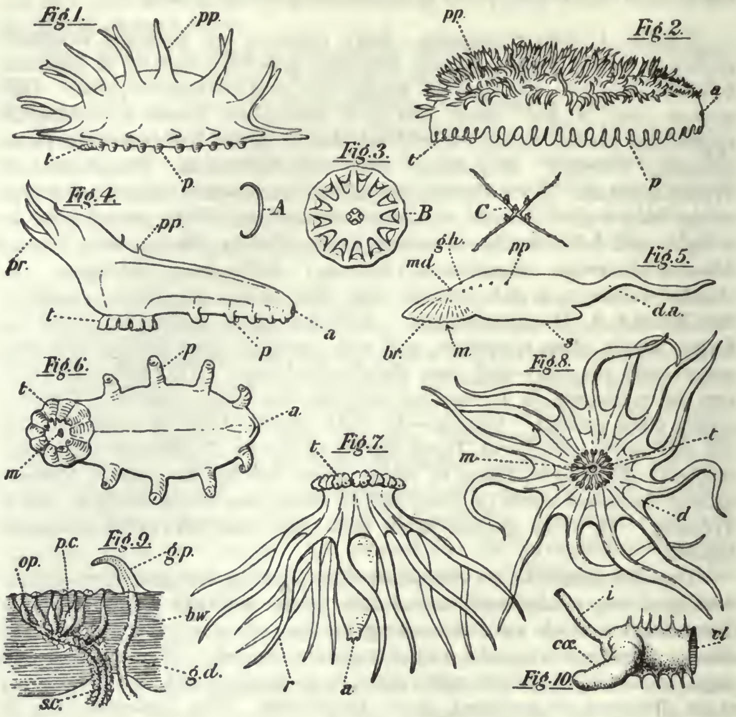


Fig. III.

1.—Left side view of *Deima validum*, Théel. (After Théel.)
2.—*Ilyodaemon maculatus*, Th. (After Théel.)
3.—(A) C-shaped spicule of *Scotoplanes albida*, Th.; (B) wheel of *Pannychia moseleyi*, Th.; (C) four-armed spicule of *Elpidia rigida*, Th. (After Théel.)
4.—*Peniagone wyvillii*, Th. (After Théel.)
5.—*Psychropotes longicanda*, Th. (After Théel.)
6.—Ventral view of *Elpidia glacialis*, Th. (After Théel.)
7 and 8.—Side view and oral view of *Pelagothuria natatrix*, Ludw. (Modified from Ludwig.)
9.—Section through the madreporite and genital papilla of *Ilyodaemon maculatus*, Th. (After Théel.)
10.—Portion of the intestine and rectal "cloaca," with its caecum, of *Benthodytes sanguinolenta*, Th. (After Ludwig.)
a, anus; *br*, brim; *b.w*, body-wall; *cl*, rectal "cloaca"; *coe*, caecum; *d*, disc; *d.a*, dorsal appendage; *g.d*, genital duct; *g.h*, genital aperture; *g.p*, genital papilla; *i*, intestine; *m*, mouth; *op*, opening of pore canal; *p*, tube-foot; *p.c*, pore canal; *pp*, papilla; *pr*, anterior process; *r*, ray of the disc; *s*, creeping sole; *s.c*, stone canal; *t*, tentacle.

Calcareous ring of five or ten pieces. Spicules various, frequently in the form of wheels and four-rayed spicules. Sub-Family 1. Psychropotinae. Body surrounded by a brim. Mouth quite ventral. Dorsal papillae usually small. Tube-feet small, as a rule on the three ventral radii. Calcareous ring incomplete, the interradial pieces being represented by small spicules. Genital tubes in a right and left tuft. Genera—*Psychrotrephes*, Théel; *Euphronides*, Théel; *Psychropotes*, Théel, Fig. III. 5; *Benthodytes*, Théel. SUB-FAMILY 2. DEIMATINAE. Mouth sub-ventral. Papillae large and numerous. Tube-feet large, generally only on the lateral ventral radii. Calcareous ring of five radial and five interradial pieces. Genital tubes in a right and left tuft. Genera—A. With a row of large papillae above the lateral ventral podia. Median ventral podia rudimentary or absent. Twenty tentacles—*Deima*, Théel (Fig. III. 1); *Oneirophanta*, Théel; *Orphnurgus*, Théel; *Scotodeima*, Ludwig. B. Without a distinct row of lateral ventral papillae, fifteen to twenty tentacles. Wheel spicules—*Laetmogone*, Théel; *Ilyodaemon*, Théel (Fig. III. 2; *Pannychia*, Théel; *Capheira*, Ludwig. SUB-FAMILY 3. ELPIDIINAE. Mouth generally sub-ventral. Papillae usually few and large. Podia only on the lateral ventral radii. Calcareous ring of five radial pieces. Genital tubes in one or two tufts. Genera—A. With ten tentacles—*Parelpidia*, Théel; *Elpidia*, Théel (Fig. III. 6); *Scotoplanes*, Théel; *Kolga*, Dan. and Koren; *Irpa*, Dan. and Koren; *Peniagone*, Théel (Fig. III. 4); *Scotoanassa*, Théel. B. With more than ten tentacles—*Achlyonice*, Théel; *Enypniastes*, Théel.

The Elpidiidae are a deep-sea group of wonderfully diverse outward form. The body is generally flat or even concave ventrally; it is often produced along its lateral edge into a brim, which may be posterior (as in *Scotoplanes*), anterior (as in *Elpidia purpurea*, Théel), both anterior and posterior (as in *Scotoanassa*), or all round (as in the *Psychropotinae*). The mouth may be quite ventral, and some way behind the anterior edge of the body (Fig. III. 5). The anus is terminal, dorsal, or ventral. Tube-feet occur on the ventral radii only, and are often remarkable for their large size and paired arrangement (Fig. III. 6), resembling the feet of a segmented animal. The dorsal papillae also may be distinctly paired and very large (Fig. III. 1). Peculiar posterior dorsal appendages, sometimes of huge size (Fig. III. 5), are developed in *Euphronides* and *Psychropotes*. Somewhat similar anterior appendages occur in *Peniagone* (Fig. III. 4). These outgrowths of the body-wall are often supplied with right and left canals from the radial, water-vascular system. The most characteristic spicules are C-shaped, four-armed wheels (Fig. III. 3), and perforated plates. The calcareous ring is generally but slightly developed; in the Elpidiinae the five radial pieces only are represented as single-branched spicules. Auditory vesicles or otocysts are sometimes situated in the Elpidiinae along the circular and radial nerves, but chiefly along the lateral ventral radii. Of great interest is the relation of the stone-canal to the body-wall in this family. The primitive condition in which it opens by a single pore in front of the genital aperture is found in *Elpidia* (some species), *Kolga*, and other genera. In some forms, *e.g.* *Laetmogone* and *Ilyodaemon* (Fig. III. 9), it opens by a number of pores to the exterior. The external opening has been lost in *Irpa*, *Benthodytes*, and others, the canal opening to the coelom, but being still connected with the body-wall. There are no retractor muscles, and no Cuvierian organs. Although the Elpidiidae differ from the preceding family by the generally simple, unpaired structure of the longitudinal muscles (p. 224), and the absence of well-developed respiratory trees (pp. 222, 225), yet they are undoubtedly closely related to them, and more especially to the Synallactinae.

FAMILY 3. PELAGOTHURIIDAE. Body cylindrical, and produced at the base of the crown of tentacles into an umbrella-like disc, drawn out into long slender rays. Mouth and anus terminal. No podia; branches of the tentacle canals extending into the rays of the disc. No retractors and no respiratory trees; a single stone-canal opening to the exterior. Right and left tufts of genital tubes. No calcareous skeleton. Genus—*Pelagothuria*, Ludwig (Fig. III. 7 and 8), represented only by a remarkable free-swimming Holothurian, *Pelagothuria natatrix*, recently discovered in the Pacific. The thirteen to sixteen tentacles are forked and beset with papillae, and the disc is produced into a corresponding number of rays, each containing a branch of the tentacular canal. These rays may represent the modified tentacular ampullae of the Holothuriidae; or the disc may be derived from the anterior brim, which occurs in the two preceding families. The five radial vessels are normally developed, in spite of the absence of podia. The longitudinal muscles are in simple bands. Neither calcareous ring nor calcareous spicules are developed.

This highly modified form undoubtedly belongs to the Actinopoda, since there are radial canals, and the circular muscles are interrupted at the radii. The absence of respiratory trees, and of free tentacular ampullae, and the simple longitudinal muscles remove it from the Molpadidae; whilst the first of these characters, combined with the absence of podia and retractors, separate it from the Cucumariidae. With the Elpidiidae, on the other hand, it has many characters in common, such as the single stone-canal opening to the exterior, the simple longitudinal muscles, the absence of respiratory trees, and the reduction of free tentacular ampullae and the calcareous ring. *Pelagothuria*, therefore, is probably a free-swimming form derived from an Elpidiid ancestor.

FAMILY 4. CUCUMARIIDAE. Podia generally tube-feet only and no papillae. Mouth and anus terminal or dorsal. Tentacles eight to thirty, branched. Tentacle ampullae rudimentary or absent. Madreporite internal. Calcareous ring of five radial and five interradial pieces. Retractor muscles. Longitudinal muscles generally simple. Respiratory trees well developed. Cuvierian organs rare. Right and left tufts of genital tubes. Spicules chiefly rods and knobbed, perforated plates. Genera—A. With distinct creeping sole. Ventral podia restricted to radii — *Colochirus*, Troschel; *Psolidium*, Ludwig; *Theelia*, Ludwig (Fig. IV. 10); *Psolus*, Oken (Fig. IV. 8). B. Without distinct creeping sole—*Thyone*, Oken (Fig. IV. 11); *Orcula*, Troschel; *Phyllophorus*, Grube; all with scattered podia (generally). With podia more or less restricted to the radii; *Cucumaria*, Blainville (Fig. IV. 1, 2, 3, 4, and 5; *Pseudocucumis*, Ludwig; *Actinocucumis*, Ludwig; *Echinocucumis*, Sars; *Sphaerothuria*, Ludwig (Fig. IV. 9). C. Flask-shaped, with mouth and anus close together—*Rhopalodina*, Gray (Fig. IV. 7).

The Cucumariidae are distinguished by the possession of delicate retractile arborescent tentacles (Fig. IV. 3 and 4). Frequently the two median ventral tentacles are smaller than the others (Fig. IV. 3), as in species

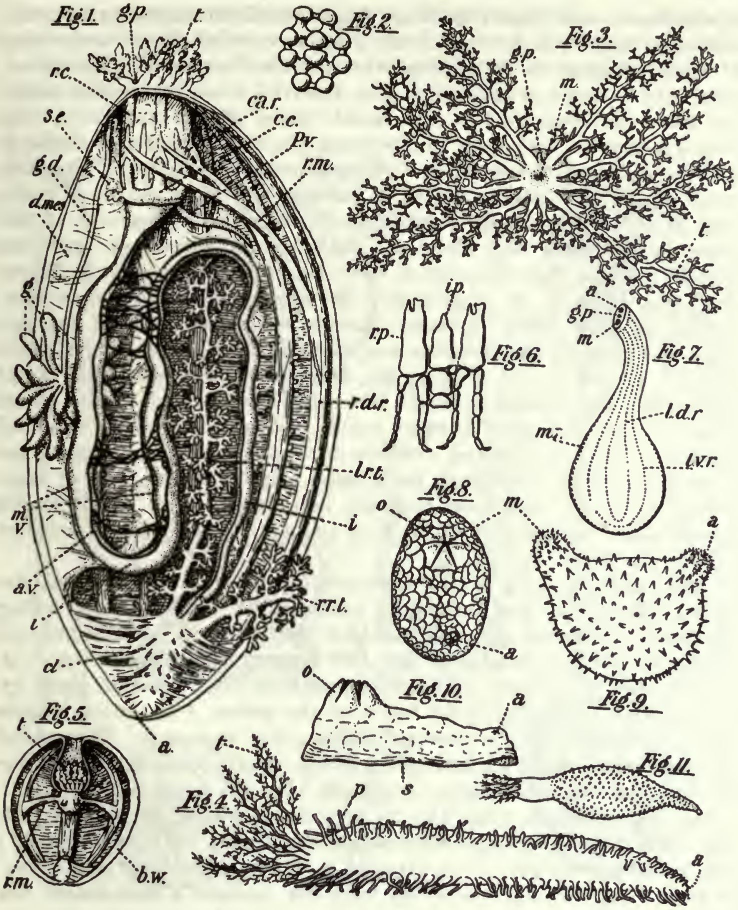


Fig.1.
g.p.
t.
r.c.
s.e.
ca.r.
c.c.
p.v.
r.m.
g.d.
d.me.
g.
r.d.r.
l.r.t.
m.v.
i
a.v.
r.r.t.
i
cl
a.
Fig.2.
Fig.3.
g.p.
m.
t.
i.p.
r.p.
Fig.6.
a.
g.p
m
Fig.7.
l.d.r
m.r.
l.v.r.
Fig.8.
o
m
a
a
Fig.9.
o
Fig.10.
a
s
Fig.11.
Fig.5.
t
r.m.
b.w.
t
Fig.4.
p
a

Fig. IV.

1.—*Cucumaria pentactes* (Linn.), opened along the right of the median dorsal line; the right respiratory tree has been cut short. 2.—Spicule; 3.—Oral view; and 4.—Left side view of the same.

5.—Inner view of a retracted *C. pentactes*, from which the dorsal region of the body-wall has been removed, and the viscera extracted, to show the action of the retractor muscles.

6.—Portion of the calcareous ring of *Orcula tenera*, Ludw. (After Ludwig.)

7.—Diagrammatic drawing of *Rhopalodina lageniformis*, Gray. (After Lang.)

8.—"Dorsal" view of *Psolus antarcticus* (Philippi). (After Théel.)

9.—Left side view of *Sphaerothuria bitentaculata*, Ludw. (After Ludwig.)

10.—*Theelia ambulatrix*, Bell.

11.—*Thyone fusus* (O. F. Müller).

a, anus; *a.v*, anti-mesenterial blood-vessel; *b.w*, body-wall; *ca.r*, calcareous ring; *c.c*, circular water-vascular canal; *cl*, cloaca; *g*, gonad; *g.d*, genital duct; *g.p*, genital pore; *i*, intestine; *i.p*, interradial piece; *l.d.r*, left dorsal radius; *l.r.t*, left respiratory tree; *l.v.r*, left ventral radius; *m*, mouth; *m.r*, median ventral radius; *m.v*, mesenterial blood-vessel; *p*, podium; *p.v*, polian vesicle; *r.c*, radial canal; *r.d.r*, right dorsal radius; *r.m*, retractor muscle; *r.p*, radial piece; *r.r.t*, right respiratory tree; *s*, creeping sole; *s.c*, stone canal; *t*, tentacle.

of *Cucumaria* and *Psolus;* in other cases several tentacles may be small, and these may even form an inner ring surrounded by an outer ring of large tentacles, as in *Phyllophorus* and *Pseudocucumis.* The stone-canal may be single or multiple. Five powerful retractor muscles, reaching from the body-wall to the radial pieces of the calcareous ring (Fig. IV. 1 and 5, *r.m*), serve to invaginate the anterior region of the body so as to withdraw the mouth and tentacles out of sight (Fig. IV. 5). The body-wall in the anterior region is thinner and often devoid of podia (Fig. IV. 11). Every stage is exhibited between the arrangement of the podia in a double row along the radii, as in *Cucumaria pentactes* (Fig. IV. 4), and their distribution over the interradial areas, as in *Thyone fusus* (Fig. IV. 11). In *Theelia* they are nearly, and in *Psolus* entirely, reduced on the "dorsal" surface. This is correlated with the development of a very distinct creeping sole, to which the podia are restricted (Fig. IV. 10 and 8). In these genera the calcareous deposits in the dorsal region form large plates or scales; five triangular so-called "oral" plates close over the introverted anterior region, and small plates may surround the anus. In *Colochirus* and *Actinocucumis* somewhat similar valves are developed in front. Although the spicules may be in the form of large perforated plates, sometimes produced into spines, as in *Sphaerothuria bitentaculata*, Ludwig (Fig. IV. 9), they are more usually rods or knobbed buttons and plates (Fig. IV. 2).

The calcareous ring in the Cucumariidae is very well developed, the pieces being large, and frequently made up of several plates fitting together. The radial segments, to which the retractors are attached, are generally produced backwards into two long processes (Fig. IV. 6). A more or less pronounced bilateral symmetry is often brought about by the unequal development or fusion of the pieces. Cuvierian organs have been described in *Cucumaria frondosa* and *C. nigricans.* The genital tufts are paired, and lead into a duct which usually opens to the exterior on a papilla within the circlet of tentacles (Fig. IV. 1 and 3, *g.p*).

In *Sphaerothuria* (Fig. IV. 9) the dorsal surface is reduced, the mouth and anus being approximated and the ventral radii much curved; this process is carried to an extreme in the extraordinary genus *Rhopalodina* (Fig. IV. 7), where the body has assumed a flask-shape, the mouth and anus are close together at the small end, while the radii are bent round. This appearance misled the early observers, who described *Rhopalodina* as having ten radii.

Whilst the Cucumariidae resemble the Holothuriidae in the possession of well-developed respiratory trees, they differ markedly from all the preceding families in the shape of the tentacles and the presence of retractor muscles.

FAMILY 5. MOLPADIIDAE. Neither tube-feet nor papillae. The posterior region generally tapering. Mouth and anus terminal. Generally fifteen simple or digitate tentacles. Tentacle ampullae well developed. Calcareous ring of five radial and five interradial pieces. Single stone-canal with an internal madreporite. Longitudinal muscle bands more or less paired. Respiratory trees present; Cuvierian organs rare. Genital tubes in right and left tufts. Genera—A. With well-developed retractor muscles; tentacles digitate—*Molpadia*, Cuvier. B. Retractors absent or rudimentary—*Eupyrgus*, Lütken; *Haplodactyla*, Grube; *Caudina*, Stimpson; *Trochostoma*, Dan. and Kor.; *Ankyroderma*, Dan. and Kor. (Fig. I. 10).

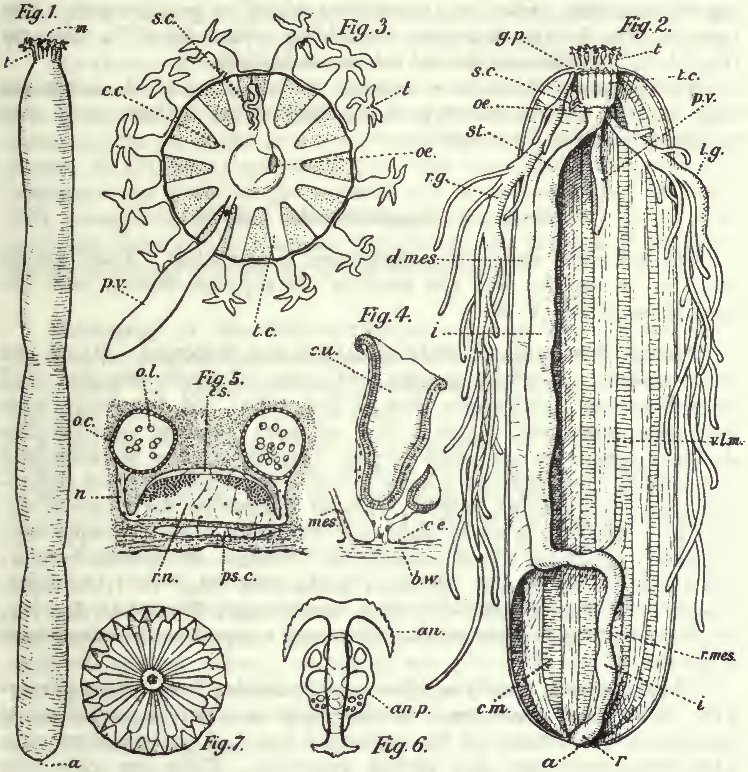


Fig. V.

1.—Left side view of *Synapta digitata*, Mont.
2.—The same opened up to the right of the median "dorsal" line.
3.—Diagram of the water-vascular system of *S. digitata* illustrating the Paractinopod plan.
4.—Ciliated urns; and
5.—Transverse section through the radius and otocysts of *S. digitata*. (After Cuénot.)
6.—Anchor and anchor-plate of *S. digitata*.
7.—Wheel of *Myriotrochus Rinkii*, Steenstrup. (After Danielssen and Koren.)

a, anus; *an*, anchor; *an.p*, anchor-plate; *b.w*, body-wall; *c.c*, circular canal; *c.e*, coelomic epithelium; *c.m*, circular muscles; *c.u*, ciliated urn; *d.mes*, dorsal mesentery; *e.s*, epineural sinus; *g.p*, genital pore; *i*, intestine; *l.g*, left gonad; *m*, mouth; *mes*, mesentery; *n*, nerve; *o.c*, otocyst; *oe*, oesophagus; *o.l*, otolith; *ps.c*, pseudhaemal canal; *r*, rectum; *r.g*, right gonad; *r.mes*, right mesenterial fold; *r.n*, radial nerve; *s.c*, stone-canal; *st*, stomach; *t*, tentacle; *t.c*, tentacle canal; *v.l.m*, median ventral longitudinal muscle.

The Molpadiidae are rounded forms, with generally a tapering, tail-like, posterior end. The tentacles are simple processes, or of lobed or digitate shape. Their ampullae are large and free, except in *Eupyrgus* (?). There are no podia, unless they be represented by the anal papillae. As in the preceding family, the calcareous ring is well developed, often bilaterally symmetrical, and with radial pieces strongly forked behind. In *Trochostoma* and *Ankyroderma* the stone-canal is still connected with the body-wall. Cuvierian organs have been described in *Molpadia chilensis*, J. Müll. The calcareous spicules are very similar to those of the Cucumariidae, except in *Ankyroderma*, which has peculiar anchor-like spicules (Fig. I. 11), somewhat resembling those found in *Synapta* (Fig. V. 6). *Trochostoma* has red calcareous deposits.

The presence of retractor muscles, the structure of the calcareous ring, and the general anatomy of the Molpadiidae indicate their close relationship to the Cucumariidae.

ORDER 2. **Paractinopoda**, Ludwig.

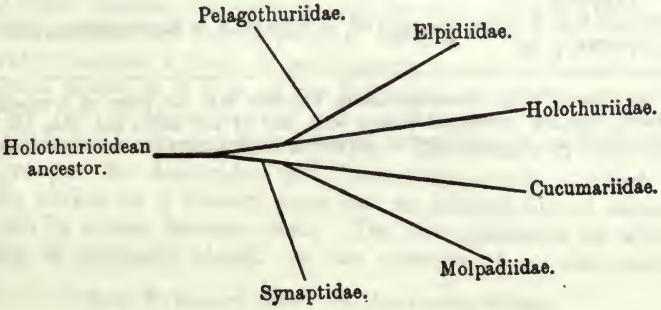
The five radial canals have disappeared in the adult. There are no tube-feet or papillae, and the tentacles are supplied directly from the circular canal (Fig. V. 3).

FAMILY, SYNAPTIDAE. Body cylindrical and elongated. Mouth and anus terminal. Tentacles pennate or digitate. Tentacle ampullae small or rudimentary. Calcareous ring of five radial, and frequently more than five interradial, pieces. One or more internal madreporites. Auditory vesicles on the radial nerves. Circular muscles uninterrupted at the radii. Longitudinal muscles as a rule unpaired. Neither respiratory trees nor Cuvierian organs. Ciliated funnels on the coelomic epithelium. Genital tubes in right and left tufts, often hermaphrodite. Calcareous spicules as wheels, anchors, etc. Genera—A. Spicules various; no wheels in the adult. *Synapta*, Eschscholtz (Fig. V. 1); *Anapta*, Semper. B. With wheels—*Chiridota*, Eschscholtz; *Trochodota*, Ludwig; *Trochoderma*, Théel; *Myriotrochus*, Steenstrup; *Acanthotrochus*, Danielssen & Koren.

The tentacles of the Synaptidae vary in number from ten to twenty-five. When they exceed ten in number there is usually a corresponding increase in the number of the interradial pieces of the calcareous ring. The radial pieces are often pierced anteriorly. There are some very characteristic spicules, such as the many-spoked "wheels" (Fig. V. 7) of some genera (and in the larva of *Synapta*), and the anchors and anchor-plates in *Synapta* (Fig. V. 6, *an*, *an.p*). The perforated anchor-plates lie in the cutis parallel with the surface, whilst the "shank" of the anchors rest against them, the "arms" projecting towards the surface. They aid locomotion (Östergren, 1897). A pair of auditory vesicles, or otocysts, has been found at the base of the five radial nerves in *Synapta* and other forms (V. *o.c*). Sense organs, some pigmented and perhaps representing eyes, occur in some species on the tentacles. The radial water-vascular canals, which are absent in the adult, are temporarily developed in the larva (Fig. I. 8, *r.c.c*). The tentacular canals, coming from the circular canal, may branch and supply several tentacles. The layer of circular muscles is not interrupted at the radii, as in the *Actinopoda*. Retractor muscles are developed in some species of *Synapta* and *Chiridota*. Very remarkable are the funnels or ciliated urns (Fig. V. 4, *c.u*) situated on the mesentery, and sometimes also on the inner surface of the body-wall. These cup-shaped organs, the function of which is obscure, are attached by stalks to the epithelium, and may be joined together into large bunches (*Chiridota*). The genera *Synapta*, *Anapta*, *Chiridota*, and *Trochodota* are hermaphrodite. The genital pore is situated behind the tentacles (Fig. V. 2).

The absence of radial water-vascular canals, and of interruptions in the circular musculature, as well as the presence of ciliated urns, distinguish the Synaptidae from all the preceding families. The first of these characters has no doubt been secondarily acquired, since the canals are present in the larva; correlated with this reduction is the method of progression by means of the tentacles and of contractions of the body-wall, accompanied by the entire disappearance of podia. On the other hand, the shape of the tentacles, the spicules, the presence of retractors, indicate a distant relationship to the Molpadiidae.

Phylogeny of the Holothurioidea.—It has been shown above that the Actinopod Holothurians fall into two groups. In the first, containing the Holothuriidae, Elpidiidae, and Pelagothuriidae, the tentacles are more or less peltate; the calcareous ring is radially symmetrical and of simple structure, it may be reduced and even absent; the stone-canal often retains its primitive opening to the exterior; the genital tubes are sometimes restricted to the left side; there are never retractor muscles. In the second group, containing the Cucumariidae and Molpadiidae, the tentacles are simple or branched, never peltate; the calcareous ring is much developed, with posterior prolongations, and often bilaterally symmetrical; the stone-canal always opens internally; there are always right and left tufts of genital tubes; retractors are generally developed. The two groups, then, probably represent two diverging stems, arising from a common ancestor possessed of respiratory trees. The Synaptidae would appear to have come off far down the Cucumarian stem, perhaps in common with the Molpadiidae. These relationships may be expressed in the following diagram :—



Little is known concerning the origin of the class. It may, however, safely be conjectured that the Holothurians are derived from an Echinoderm ancestor with five typically developed radii, along which ran branches of the nervous and water-vascular systems, the latter provided with podia. The outward bilateral symmetry of the Holothurians seems to have been secondarily acquired in connection with their free-moving mode of life.[1]

LIST OF WORKS.

1. *Baur, A.* 1864. (Beiträge zur Naturgeschichte der *Synapta digitata.*) Nova Acta Acad. Leop.-Carol. vol. xxxi.
2. *Bury, H.* 1889. (Studies in the Embryology of Echinoderms.) Quart. Journ. Micr. Sci., n.s., vol. xxix. pp. 409-449, pls. xxxvii.-xxxix. 1895. (The Metamorphosis of Echinoderms.) *Op. cit.* vol. xxxviii. pp. 45-135, pls. iii.-ix.
3. *Hamann, O.* 1883. (Beiträge zur Histologie der Echinodermen. I. Die Holothurien (Pedata), u.s.w.) Zeit. f. Wiss. Zool. vol. xxxix. pp. 145-190, pls. x.-xii. (II. Das Nervensystem der Pedaten Holothurien. Die Cuvierschen Organe. Nervensystem und Sinnesorgane der Apedaten), *tom. cit.* pp. 309-333, pls. xx.-xxii.
4. *Hérouard, E.* 1889. (Recherches sur les Holothuries des côtes de France.) Arch. Zool. Expér. (2), vol. vii. pp. 535-704, pls. xxv.-xxxii.
5. *Ludwig, H.* 1889-92. (Die Seewalzen.) Bronn's Klassen und Ordnungen des Thierreichs, Echinodermen, I. Klasse. [Gives a full Bibliography.]
6. —— 1894. (Reports on an exploration . . . by the . . . *Albatross* . . . XII. The Holothurioidea.) Mem. Mus. Harvard, vol. xvii. No. 3.
7. *Selenka, E.* 1867. (Beiträge zur Anatomie und Systematik der Holothurien.) Zeit. f. Wiss. Zool. vol. xvii. pp. 291-374, 4 pls.
8. —— 1876. (Zur Entwickelung der Holothurien.) *Ibid.* vol. xxvii. pp. 155-178, pls. ix.-xiii.
9. *Semon, R.* 1888. (Die Entwickelung der *Synapta digitata.*) Jena. Zeitschr. vol. xxii. pp. 175-309, pls. vi.-xii.
10. *Semper, C.* 1868. Reisen in Archipel der Philippinen. II. Theil. Vol. i. Holothurien, Leipzig.
11. *Théel, Hj.* 1882, 1886. (Report on the Holothurioidea.) *Challenger* Reports, Zoology, vol. iv. part xiii., and vol. xiv. part xxxix.
12. *Tiedemann, F.* 1816. Anatomie der Röhren-Holothurie, u.s.w. Fol. Landshut.

See also Nos. 2, 3, 19, 25*a*, and 28, in Literature of Echinoderma generally, Chapter VIII. p. 35.

---

[1] See Chapter VIII. It should not be forgotten that the plane of symmetry of the adult does not correspond exactly with that of the larva, and that the alimentary canal and the mesentery are invariably twisted spirally from left to right.

CHAPTER XIV.

THE STELLEROIDEA.[1]

CLASS II. STELLEROIDEA.

SUB-CLASS 1. ASTEROIDEA.
  Order 1. **Phanerozonia.**
  „ 2. **Cryptozonia.**

SUB-CLASS 2. OPHIUROIDEA.
  Order 1. **Lysophiurae.**
  „ 2. **Streptophiurae.**
  „ 3. **Cladophiurae.**
  „ 4. **Zygophiurae.**

THE class of the Stelleroidea includes the starfish, brittle stars, sand stars, basket-fish, and branching stars, all of which are characterised by a depressed stellate body composed of a central disc, whence radiates a number of rays or arms. They have radiately arranged genital organs (*i.e.* are actinogonidial); they are not attached by the aboral surface, nor is the oral surface furnished with ciliated food-grooves (*i.e.* are eleutherozoic); and they usually have the podia limited to the lower half of the body (*i.e.* are lysactinic), instead of having them continued upward to the apical plates, as in typical sea-urchins (which are desmactinic). The radial water-vascular vessels lie along the under sides of the arms, and are exterior to the ambulacral ossicles. The aperture of the water-vascular system or madreporite is not connected with the apical plates, as it is in all the Echinoids except *Echinocystis*.

This list of characters is quite sufficient to mark off the Stelleroids from all other Echinoderms. The class is divided into two groups—the Asteroidea and Ophiuroidea—each of which is usually ranked as a distinct class, but no definite line of separation can be drawn between them. The two characters on which reliance is generally placed are the presence of an ambulacral groove in the Asteroids and its absence in Ophiuroids; and the restriction of the digestive and generative organs to the disc, and consequent sharp distinction between body and arms, in the latter. The first character is unreliable, as in the living *Ophioteresis* there are no ventral plates, and a shallow ambulacral furrow is accordingly present. One order of fossil Ophiuroids—the *Lysophiurae*—has the same feature more strongly marked. The differentiation of the body into disc and arms happens in most Ophiuroids, but also in some Asteroids, *e.g. Freyella.* The restriction of the digestive organs to the disc appears to offer a more reliable character; but in *Astrophiura* the arms are sharply marked off from the disc and contain no digestive caeca, while the ambulacral ossicles are asteroid. Similarly the digestive and genital systems of the Asteroids, *Colpaster*, and some species of *Freyella* must be limited either to the well-marked disc, or at most to the bases of the arms; while the arm structure is practically identical with that of some Palaeozoic Ophiuroids. It must be remembered, moreover, that the digestive sac of Ophiuroids is marked by a series of radial bulgings, which may be homologous with the radial caeca of Asteroids. The position of the madreporite is relied on by Perrier, but it will not serve; in the Asteroids, *Asterina*, and *Palasteriscus* it is ventral, as in most Ophiuroids.

---

[1] By J. W. Gregory, D.Sc. MS. closed at end of 1896.

Not only is there no character which serves to separate the Ophiuroids and Asteroids, but the whole structure of the body is on the same plan in both groups. It consists in both of a central disc and a series of (usually five) radial rays. The skeleton in each ray consists essentially of two series of plates—the ambulacral and adambulacral. The former lie internal to the radial water-vascular vessel, and the furrow which this occupies is laterally protected by the adambulacral plates. Additional elements may occur, but are not found in all members of either division. The mouth armature consists of a ring round the mouth, formed by the union of one or more pairs of ambulacral and adambulacral plates for each arm, and bearing spines modified to serve as teeth. The body is protected by accessory plates or granules in the integument; these plates may be protected by spines and pedicellariae.

The alimentary system consists of a central digestive sac, opening by a mouth at the centre of the ventral surface; the size of the digestive sac is increased by radial bulgings, of which there are as many pairs as the Stelleroid has arms; these bulgings may be short and limited to the disc or base of the arms, or extend up the arms. There may or may not be an anus.

The water-vascular system consists of a ring round the oesophagus; a radial vessel runs up each arm from the ring, which also bears a series of Polian vesicles, or sac-like diverticula. The radial vessels give off a pair of branches in each segment; each branch ends in a podion, which may be pointed, or may end in a sucker. Connected with each podion there may be a globular ampulla (absent from some Asteroids, *e.g. Brisinga* and from all Ophiuroids). The madreporite in either group is dorsal, marginal, or ventral. The nervous system comprises a circumoesophageal ring and a radial branch along each arm or ray.

The reproductive organs consist of strands connected with the axial coelomic system; there is a central ring whence a pair of strands pass to each ray. A number of small gonads occur on each strand; the gonads of each strand may be grouped into one bundle, with a common aperture at the margin of the disc (as in the Asteroid *Asterias* and the Ophiuroid *Ophiothrix*); or they may occur only at the bases of the arms, as in *Freyella;* or they may occur as a series of distinct gonads with separate apertures, as in *Brisinga* and *Ophiactis.* In most Ophiuroids the gonads discharge into a bursa.

As both Ophiuroids and Asteroids are therefore constructed upon the same fundamental plan, as they contain the same variations from the typical arrangement, and as there is not a single constant difference between them, it seems indispensable that they should be united into one class, the STELLEROIDEA, which may be diagnosed as follows:—

Eleutherozoic, actinogonidial, and lysactinic Echinoderma in which ambulacral plates lie internal to the radial ambulacral vessels. The madreporite is not connected with an apical system of plates. The body is more or less depressed, and is markedly stellate.

In spite of the fact that the separate treatment of the Asteroids and Ophiuroids has led to many unfortunate errors, and still hampers the classification of the group, it seems advisable here to consider the sub-classes separately.

SUB-CLASS 1. ASTEROIDEA.

The sub-class Asteroidea includes the Echinoderms known as Starfish. The animals consist of a central body marked on the ventral side by a series of radial furrows which are usually continued outward along prolongations of the body known as arms. They live on the sea-floor and creep about by means of suckers or podia in the radial furrows, the side containing which is always placed downwards. The general aspect of starfish is therefore very different from that of any of the previously described groups of Echinoderms. They are closely related to the Ophiuroids, and no very satisfactory line of demarcation can be drawn between the two sub-classes; but the Asteroids usually have diverticula from the alimentary canal extending along the arms, which pass gradually into the disc.

Before 1841 the Asteroids and Ophiuroids were always considered members of one group. Thus J. H. Linck (23), who in 1733 began the systematic study of the Stelleroids, included members of both sub-classes in his group "Stella." He separated the Asteroids as the *Stellae fissae*, which he divided according to the number of arms or rays into such divisions as *Trisactis*, *Tetractis*, *Hexactis*, etc. Linnaeus in 1766 included both sub-classes as well as some unstalked Crinoids in his genus *Asterias*, grouping all the starfish together as "Stellatae." Lamarck in 1816 (21), de Blainville (1830 and 1834), Nardo and Brandt (1834), and L. Agassiz (1835) proposed various divisions of *Asterias*, which these authors recognised to be a family or order. In 1840 Gray's *Synopsis*, and Müller and Troschel's essay, *Ueber die Gattungen der Asterien* (35), first prepared the way for a scientific classification. In 1842 the latter authors' *System der Asteriden* (36) laid the foundation for all later work.

After that date additions to our knowledge of the recent Asteroids have been made by many authors, especially A. Agassiz, Barrett, Bell, Danielssen, Fewkes, Forbes, Gray, Jullien, Koren, de Loriol le Fort, Lütken, Marenzeller, Martens, Moebius, Perrier, Philippi, Sars, Sladen, E. A. Smith, Stimpson, Studer, Thompson, Verrill, Viguier. The fossil forms have been described by E. Billings, Eck, Forbes, E. Fraas, Goldfuss, Heller, Hall, de Loriol le Fort, Müller, C. F. Roemer, Salter, Simonowitsch, Stürtz, Wright, and others.

The study of the anatomy of Asteroids received its first stimulus from the researches of Joh. Müller (34). The skeleton has been described by Meckel (1828), Duvernoy (1848), Gaudry (13), and especially Viguier (52). Perrier has devoted most attention to the pedicellariae (1875 and 1884). The study of the visceral anatomy was begun by Tiedemann, Delle Chiaje, and Meckel; and of the nervous system by Krohn. The present position of the subject is due mainly to Ludwig (25), Cuénot (8, 9), and Hamann (17).

The embryology has been worked out by many authors, the study of the early stages being unusually easy; among contributions to this branch of the subject are those of Joh. Müller (1848 - 55), A. Agassiz (1877), Ludwig (1882), MacBride (1893 and 1894), (32, 33), and Bury (1889 and 1895).

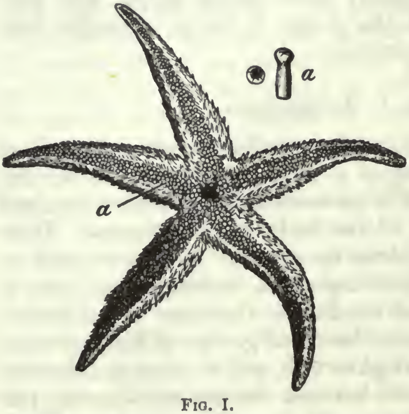


Fig. I.
Actinal surface of *Asterias rubens* with a podion (*a*) enlarged.

The principal classifications after those of Gray, and of Müller and Troschel, are those of Viguier (1878), (52), based on the oral skeleton, of Perrier (1884 and 1894), (38), on the pedicellariae, and of Sladen (1889), (48).

Structure of a Typical Asteroid.—The common English starfish (*Asterias rubens*, L.) is a convenient type of the Asteroidea. It has a flattened body composed of a central disc from which radiate five arms (Fig. I.). The upper or abactinal surface of the Body is covered by an integument or perisoma (Fig. II.), composed of a network of calcareous rods, the meshes between which are closed by tough membrane. The anus opens almost in the centre of the abactinal surface. Between the anus and one of the angles between the rays occurs the madreporite, a thick grooved plate, perforated by pores leading to the water-vascular system.

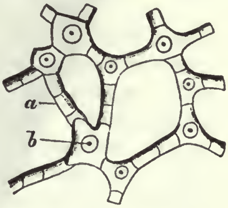


FIG. II.
Asterias rubens, part of abactinal skeleton.

The ventral surface of each Arm is traversed by a broad groove; since the grooves radiate from the mouth to the ends of the arms, the ventral surface is known as the actinal surface. The mouth is at the centre of this side of the body, and is surrounded by spines (the "mouth papillae"). The grooves are occupied by four rows of suckers or podia, and therefore correspond to the ambulacral areas of the Echinoid. On either side of the grooves are three rows of spines.

Dissection is necessary for the recognition of any further points in the structure of the *Asterias*. By the removal of some of the podia, the ambulacral grooves may be seen to lie outside a series of pairs of narrow plates—the ambulacral ossicles (Fig. III.). The two series of ossicles meet in the middle line; laterally they abut against a row of adambulacral ossicles, beyond which are further rows of interambulacral and marginal ossicles, all of which are comparatively small. The ossicles are protected by spines and pedicellariae similar to, but simpler than, those of Echinoidea.

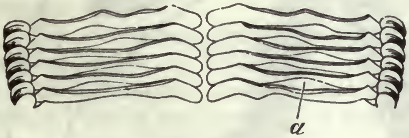


FIG. III.
Asterias rubens, ambulacral and adambulacral plates. *a*, apertures for podia.

The Oral Skeleton (or actinostomial ring) consists of a solid calcareous ring around the mouth. It is composed of thirty plates in a quinqueradiate starfish, there being always six times as many plates as there are rays. Each segment of the oral skeleton consists of two pairs of ambulacral, and of one pair of adambulacral ossicles. In *Asterias* the ambulacral plates are more prominent than the adambulacrals, and project into the oral cavity. The mouth armature is therefore on the ambulacral type (Viguier, 52).

The Alimentary System consists of a mouth at the centre of the actinal surface of the starfish. The oesophagus is very short

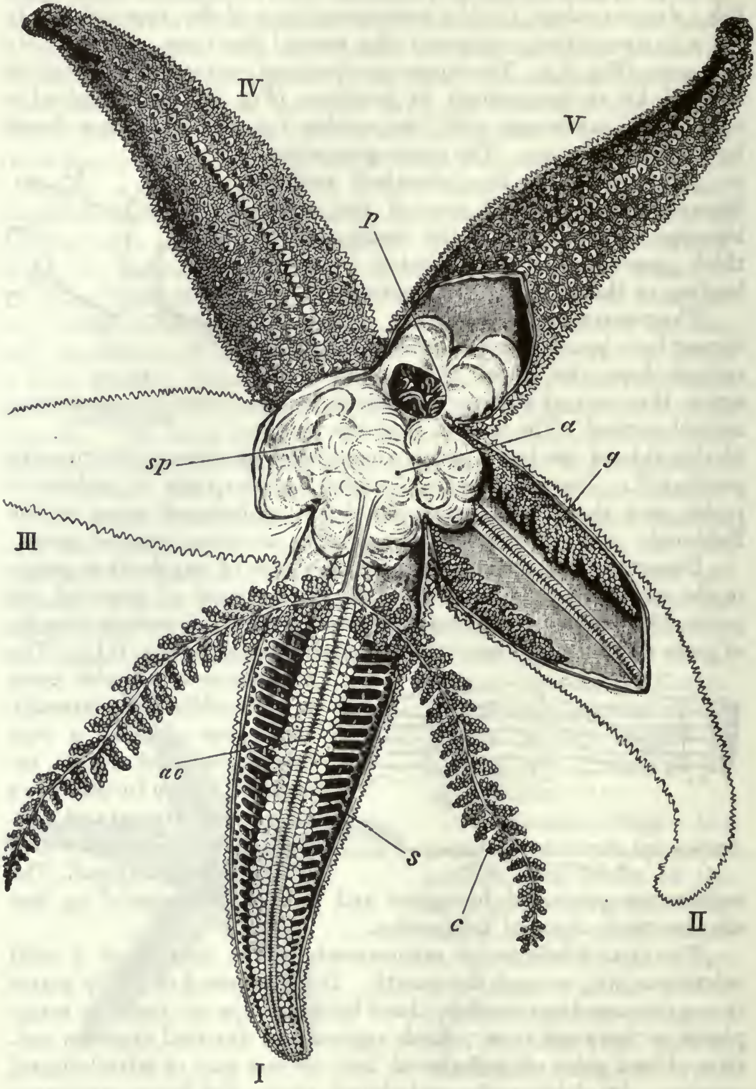


FIG. IV.

Asterias rubens. I, ray from which the skin of the abactinal surface has been removed and the outgrowths (*c*) displaced, showing the ambulacral ossicles (*ao*); the suckers (*s*), *g*, gonads in ray II; *a*, anus; *sp*, stomach, the folded arrangement of the walls of which are shown by removal of part of the upper wall at the base of ray V. From F. J. Bell, *Catalogue of British Echinoderms in the Brit. Mus.* (*Nat. Hist.*).

and leads to a large stomach, which occupies most of the disc. From the stomach five branches pass off, one to each ray. Each branch divides into two caeca, which lie one on either side of the ray. From the stomach a short rectum leads upward to the anus, which opens on the abactinal surface at a little distance from the centre. Two small longitudinally folded diverticula from the rectum occur below the anus. These rectal caeca occupy a similar position to the "respiratory trees" of Holothurians, with which they may be homologous.

The Water-Vascular System consists of a circular vessel round the oesophagus (the circumoesophageal canal or water-vascular ring), from which, in a five-rayed starfish, there are eleven offsets. The most important are the five radial canals, one of which passes along each ray, just external to the ambulacral ossicles. From these radial canals branches are given off on either side; each branch ends in a tubular podion, which consists of an internal reservoir or ampulla situated above the ambulacral ossicles, and of an external tube or sucker. Valves occur on the transverse branches, and prevent water, expelled from the ampulla, returning into the radial vessel; they thus direct it into the sucker. The next set of offsets from the circumoesophageal canal are five sac-like "Polian vesicles," one in each interradius; they act as reservoirs for the water-vascular system. The last (eleventh) vessel on the circumoesophageal canal is the "stone-canal," which runs from the base of one of the Polian vesicles to the upper surface of the starfish. It expands above, and its upper end is attached to the madreporite, through the pores in which water enters the water-vascular system.

The circumoesophageal canal also supports nine tufts of tubules known as Tiedemann's bodies; there is a pair of tufts in each interradius, one on either side of the base of the "Polian vesicle," but in the interradius containing the stone-canal there is only a single Tiedemann's body.

The presence of a blood-vascular system in Asteroids is not yet determined, the organs described as such belonging to the Pseudhaemal System (cf. pp. 22, 26). The main organ in this system is the "axial sinus," which is a rather thick vertical tube surrounding the stone-canal. It communicates below with a ring (the circumoesophageal pseudhaemal ring), which surrounds the mouth and gives off five radial branches, which pass one along the upper side of each ray. At its upper end the axial sinus communicates with the genital ring; attached to this ring are five pairs of short processes, while an additional pair passes beside a prolongation of the axial sinus leading to the madreporite. Some of the pores of the madreporite open to the axial sinus, and there is no known direct communication between the latter and the stone-canal.

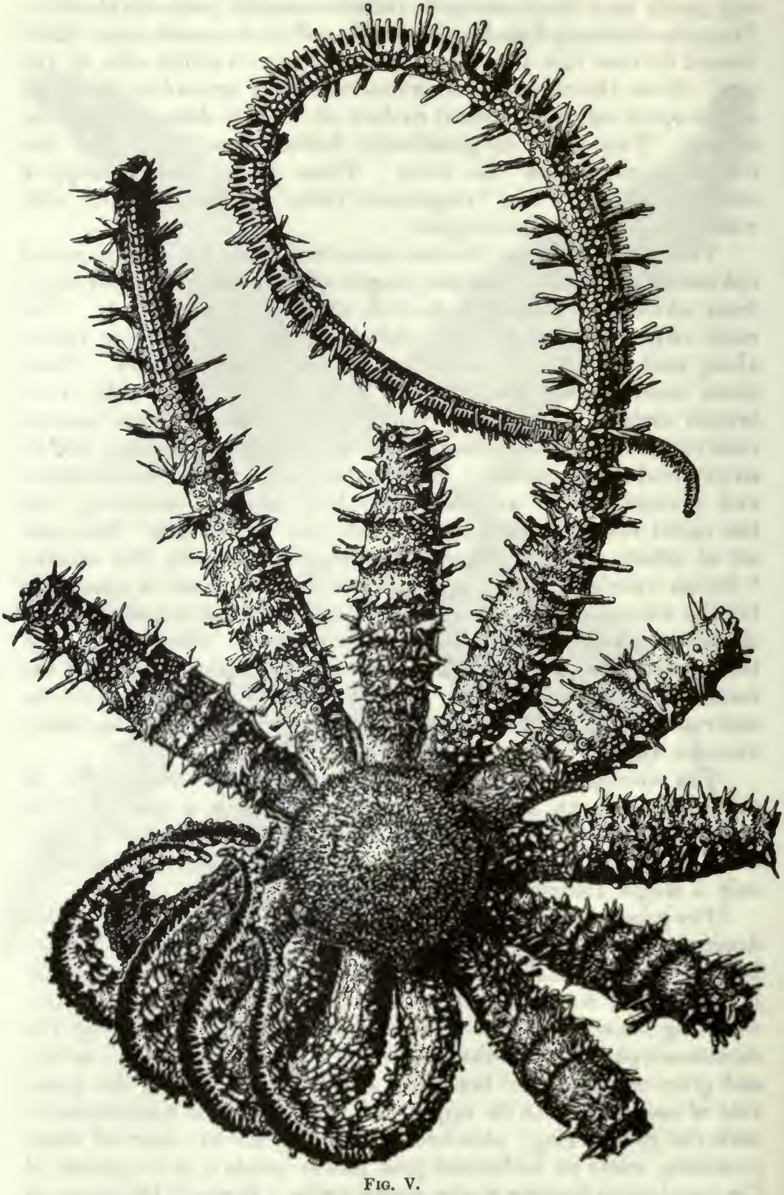


FIG. V.
Brisinga coronata. Abactinal surface.

The Nervous System consists of three disconnected sets of nerves. The most important set is composed of a circumoral ring, from which a branch runs up each ray between the rows of tube-feet, and external to the pseudhaemal radial vessel. Each branch gives off nerves to the tube-feet and ectoderm of its ray. The second set of nerves consists of bands lying internal to the radial branches of the first set; they lie along the perihaemal canal, which surrounds the pseudhaemal vessel; the branches from these nerves supply the muscles of the ambulacral ossicles. The third group of nerves is abactinal in position; there is a ring round the anus, giving off a branch along the upper side of each ray, and innervating the muscles of the body wall.

The Genital Organs of *Asterias* consist of ten branched glands, a pair being situated on the dorsal side of each ray close to the disc. Each gland has a separate aperture on the abactinal surface.

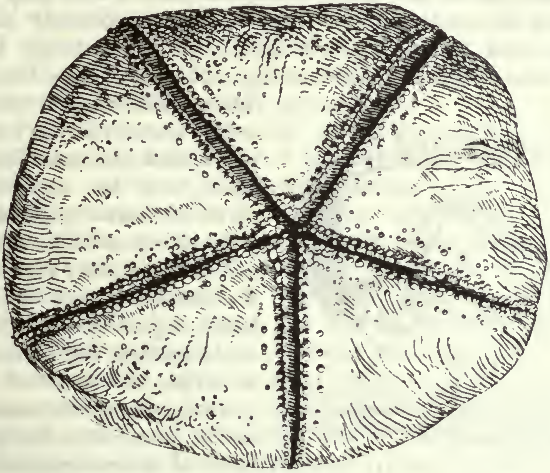


FIG. VI.
Culcita grex.

The only special respiratory organs are a series of long, tubular prolongations of the body-cavity, known as papulae, dermal branchiae, lymph gills, or branchial vesicles. In *Asterias* they occur on all sides of the rays and disc.

The most interesting sensory organ of *Asterias* is a small eye-spot on the terminal podion of each ray (Fig. XXV. on p. 30). The animal has an olfactory sense, for it will follow food, even after the eye-spots have been destroyed; the situation of this sense is diffuse, for any part of a starfish arm that can move independently will follow food (Romanes); but Prouho limits the sense of smell to a few podia near the end of the ray, which he calls "palps."

The **Variations in Structure** from the typical genus are less remarkable among the Asteroids than among the Echinoids and Ophiuroids.

In shape the extremes are genera such as *Brisinga* (Fig. V.) or *Freyella*, and *Culcita* (Fig. VI.). In the first two the arms are numerous and slender, and sharply marked off from the disc. In the last the body is bun-shaped, and the ambulacra extend for a short distance over the abactinal surface.

The most conspicuous variation from *Asterias* in skeletal structure is due to the presence of a series of thick plates round the margin both of arms and disc. These marginal plates are best developed in the order Phanerozonia. There may be two series, one above the other, and known respectively as supra-marginals and infra-marginals (Fig. VII. *d* and *c*); in some genera intermarginal plates occur between these two series. The spaces (actinal interbrachial areas) between the marginal plates and the ambulacral furrows may be occupied by a series of accessory plates, forming a pavement like mosaic.

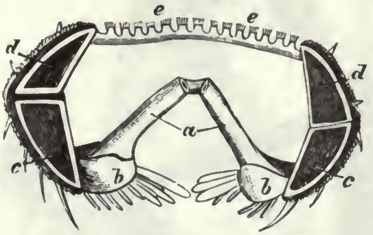


FIG. VII.

Segment of arm of *Astropecten irregularis*. *a*, supra-ambulacral plates; *b*, ambulacral plates; *c* and *d*, inferior and superior lateral plates; *e*, dorsal plates with paxillae.

The accessory plates on the abactinal side may be large or small, equal or unequal. In some species the central plate is large, and some of the remaining plates are arranged in circles round it. The plates of three of these circles have been regarded as the homologues of the calycinal plates of Crinoids, and are accordingly sometimes named the radials, basals, and infra-basals (but see p. 14). In *Cnemidiaster wyvillei* the central, and the so-called radials and basals are present; in *Zoroaster fulgens* there are infra-basals as well. The order of development of these plates is as follows:—First five plates appear round the centre of the abactinal surface; these plates move outwards to the arm-tips, and form the terminals; a second ring appears, the plates of which are the "basals"; the central plate next develops in the centre of this ring; the radial circle follows, and after that come the "infra-basals." Between the plates of the last set and the central some genera have additional plates, which cannot be homologised with any in Crinoids.

The Oral Skeleton consists of a ring of plates round the mouth. The ring is composed of as many segments as the starfish has rays, and each segment is interradial, and forms an "oral angle"; it consists of two sets of plates, usually three in number.

The oral skeleton is described as either ambulacral or adambulacral, according as the ambulacral or adambulacral plates are the more prominent. Viguier, in his important memoir on the skeleton of the Asteroids, pointed out the existence of these two types, and based his classification upon this character. As we have seen, in the genus *Asterias* the oral skeleton consists of a solid ring, in which the ambulacral plates form five prominences, while the adambulacral plates are small, and occur in the angles between them. Such a mouth-structure is described by Viguier as "ambulacral." In *Pentaceros* (*Oreaster*), on the other hand, the ambulacral plates are inconspicuous, and the adambulacral plates project into the buccal cavity and form the jaws. This type is Viguier's "adambulacral mouth." In both cases above the adambulacral plates is a basal, interbrachial, or oral plate which is called by Viguier the odontophore, although it does not bear the teeth; its value is of secondary importance.

The Pedicellariae of Asteroids are of four main types. The simplest form consists of a row of pairs of small, sessile, opposable spines; these are the "pseudo-pedicellariae." The members of the second set are "sessile." The next advance is the development of a stalk; of these pedunculate pedicellariae there are two varieties: (1) the "forficiform," in which the two hooks are attached to the nearest end of the basal plate nearest to them; (2) the "forcipiform," in which the two hooks cross one another and are attached to the end of the basal plate furthest from them. Perrier has used the pedicellariae as the basis of his classification of the Asteroids, on the ground that they are the degenerate representatives of organs once more important. Other authors, however, regard them as modified and elaborated spines, in which case they are of little taxonomic value.

Another type of spines occurs as part of the structures known as "paxillae." Each paxilla consists of a thick plate supporting a number of short, calcareous pillars, the summit of each of which is covered by a group of small spines. In some Phanerozonia, such as *Astropecten*, the paxillae occupy almost the whole abactinal surface of the Asteroid (Fig. VII.).

The Water-Vascular System is on the same plan as in *Asterias*, but there are the following modifications:—In most starfish there is a pair of Polian vesicles in each interradius; they rise from the circumoesophageal vessel beside the Tiedemann's body. The radial branches and its podia are simplified by the absence of ampullae, as in *Brisinga*, or by the podia ending in points instead of suckers, as in the Astropectinidae. Suckers are improvised in such pointed podia by a contraction of the walls below the end.

The number of madreporites is very variable among the Asteroids; in most of those with many rays there are several madreporites, but in the Solasteridae there is but one; on the other hand, many five-rayed starfish, such as *Asterias capensis*, have more than one. The stone-canal is repeated, especially in forms which reproduce asexually.

There is no anus in the Astropectinidae, the members of which are more primitive than *Asterias* in many respects. The radial caeca of the stomach remain constant, but the rectal caeca vary in number and arrangement; they are increased to five in many genera, and in *Culcita* each of the five caeca branches into two.

The "papulae" or branchial vesicles, which, in *Asterias*, rise from all parts of the external surface, are limited among Phanerozonia to the abactinal surface, and to the area enclosed by the supra-marginal plates.

The Genital Organs are, as a rule, less concentrated than in *Asterias*. The glands are repeated along the arms; in the simplest cases each series discharges its products by a single sieve-plate. The extreme case is in *Brisinga*, where there are a series of separate glands along the arm, one pair to each segment, and each gland discharges by a separate aperture.

In *Asterina gibbosa* the genital orifice is on the ventral or actinal surface, as in Ophiuroids.

The development of the Asteroids is generally indirect, the larva passing through a metamorphosis. The typical form of larva is the *Bipinnaria*, which passes through an *Auricularia* stage and thus resembles the larvae of the Holothurians rather than of the Echinoidea or Ophiuroidea (see p. 5). In some cases the Bipinnaria develops into a *Brachiolaria* by the division of the frontal process of the larva into three branches. In some genera, such as *Asterina* (the development of which has been studied with especial care), the Bipinnaria stage is never developed, although the larvae are free-swimming and undergo metamorphosis. In other cases, *e.g.* in *Blakiaster* and *Pteraster*, the development is direct; in the former case, the ova develop in "arcade-like spaces" between the paxillae of the abactinal surface; in the latter there is a large marsupium formed by the presence of a supra-dorsal membrane rising above the abactinal surface.

Asexual reproduction is not uncommon; it results either from a division of the body, approximately into halves, or by regrowth of the disc from an arm that has been thrown off. The latter method occurs especially in *Linckia*, and with the first appearance of the disc the starfish is said to assume the comet form.

Proceeding to the Systematic Description of the orders and families, we may sum up the foregoing characters in the following **Diagnosis of the Sub-Class.**[1] The Asteroidea are eleutherozoic, actinogonidial, and lysactinic Echinoderms in which there is an ambulacral groove. The arms generally pass gradually into the disc, but in some cases are sharply marked off from it. The digestive system generally has an anus, and shares in the stellate disposition of the body. Pentameric repetition is more often exceeded in this than in any other class, and asexual reproduction is not uncommon. Respiration diffuse. The madreporic aperture is generally abactinal.

---

[1] Emended from Bell (4), p. 19; the terms are explained, *antea*, p. 237.

This diagnosis at once sharply separates the Asteroids from all Echinoderms except Ophiuroids, between which, as we have seen (p. 238), it is not possible at present to draw any precise line of separation. The Asteroidea, however, always have an open actinal groove, whereas this is exceptional among the Ophiuroidea ; the arms usually pass gradually into the disc, and generally contain throughout prolongations of the genital and alimentary systems.

ORDER 1. **Phanerozonia**, Sladen.

Asteroidea with large marginal plates, and with the dermal branchiae or lymph gills limited to the abactinal surface.

This order includes a group of starfish which began in the Cambrian age and has lived on till the present time. Its members can be readily distinguished by the large size of the marginal plates. The limitation of the dermal branchiae to the abactinal surface is a more primitive condition than that met with in the Cryptozonia. Embryological evidence, and the greater importance of the order in the Palaeozoic and Mesozoic eras also suggest that this is the simpler of the two orders of starfish.

The Palaeozoic genera appear to be normal members of this order, and some of them may be included in existing families. They are, however, often all grouped together as an order, the "Palaeasteroidea," and separated from all the later, or "Euasteroidea." The character on which this separation is based is the alternation of the ambulacral ossicles in the former, whereas they are said to be always opposite in post-Palaeozoic Asteroids. This character is of great importance among Ophiuroids, for when the ossicles are alternately arranged, they cannot be united into vertebral ossicles. But when the ossicles are narrow, thin plates, closely packed into two series, one on either side of a ray, and when the separate ossicles meet those of the other side only by their narrow ends, then alternation is very likely to arise from growth pressure. In fact, one part of an arm may have the ambulacral ossicles alternate, while in another part they may be opposite. The character, moreover, is one on which little reliance can be placed when applied to fossils, for a slight movement is sufficient to alter the relative positions of the two series. It is difficult to explain the relative positions of the ambulacral ossicles in different arms of the same Asteroid, except on the assumption that the two series moved past one another during the lateral bending of the arm. Alternation of the ossicles was probably an original character ; but as the arms became flexible with the reduction of the external skeleton, and as the ambulacral ossicles became narrower, greater freedom was gained by the opposition of the two plates of a pair. The artificial nature of the divisions based on this character is shown by Stürtz's action in dividing several of his families into halves and placing members of the same family in two different orders. Thus he founded a family Palæechinasteridae for the genera *Echinasterella* and *Palasteriscus;* but he included the latter among the division with alternate ambulacral ossicles, and the former in the division in which these ossicles are opposite. As the "Palæasteroidea" include representatives of both Phanerozonate and Cryptozonate Asteroids, and of several families of each, it is necessary to dismember such an artificial group.

FAMILY 1. PALÆASTERIDAE. Phanerozonia with most or all of the ambulacral ossicles alternate; the madreporite is dorsal. Oral armament adambulacral. Abactinal skeleton tessellate. Rays long, disc small. This family includes a series of Asteroids occurring in the Lower Palaeozoic. In most of them the ambulacral ossicles are alternate, but in some cases these plates are opposite, either for a part, or for the whole length of the arm. Hence this character does not seem to be of the value assigned to it. The marginal ossicles are always conspicuous, and, as far as is known, the madreporite is fairly small and dorsal in position. The oral skeleton consists of a ring in which the adambulacral plates are most conspicuous. There are two sub-families. SUB-FAMILY 1. PALÆASTERINAE, in which the ambulacral ossicles are alternate. Genera —*Palæaster*, Hall; *Argaster*, Hall; (?) *Monaster*, Eth. jnr.; and (?) *Petraster*, Billings *pars.* The genera are all Palaeozoic, ranging from the Cambrian to the Devonian. Among existing families the nearest ally is the Archasteridae. SUB-FAMILY 2. XENASTERINAE, including those with most of the ambulacral ossicles in opposite pairs. Genera—*Xenaster*, Simonowitsch; *Tetraster*, Eth. jnr. & Nich.

FAMILY 2. PALÆASTERINIDAE. Phanerozonia with alternate ambulacral ossicles and small marginal plates. The oral armature is adambulacral. The madreporite is abactinal. The rays are short and are separated by large interradial areas. Genera—*Palæasterina*, M'Coy; *Schoenaster*, Meek & Worthen.

FAMILY 3. ASPIDOSOMATIDAE. Phanerozonia with alternate ambulacral ossicles; large marginal ossicles and large interradial areas; rays massive, petaloid, sub-petaloid, or tapering. On the abactinal surface there are large depressed areas between the marginal ossicles and the outermost of the longitudinal series of large plates which run along the arms. Genera—*Aspidosoma*, Goldf. (the type-species is *A. Arnoldi*, but as this is imperfectly known, *A. petaloides*, Simonowitsch, may be accepted provisionally); *Palaeonectria*, Stürtz; *Palaeostella*, Stürtz; *Trichasteropsis*, Eck; *Archasterias*, Mull., may belong here, but the genus is insufficiently known.

FAMILY 4. TAENIASTERIDAE. Phanerozonia with alternate ambulacral ossicles. There are neither disc nor interbrachial areas. The adambulacral plates are large and act as marginal plates. The axes of the marginal plates are parallel and the rays petaloid (as in *Stenaster*), or the axes of the marginal plates are convergent; these plates bear spines on their free ends, and the rays taper gradually (*Taeniaster*). Genera—*Taeniaster*, Billings; *Stenaster*, Billings, *pars* (*S. salteri*, but not *S. pulchellus*); both Ordovician of Canada; *Salteraster* and *Urasterella*, M'Coy, Silurian, England; *Protasteracanthion*, Stürtz, Devonian, Germany.

FAMILY 5. ARCHASTERIDAE. Phanerozonia with opposite ambulacral plates. There is an anus, but no super-ambulacral plates. Pedicellariae are generally present. The abactinal plates are spiniform or paxilliform. The adambulacral plates are large. This family includes a large number of Neozoic starfish, ranging from the Lower Oolites to the present day. They have frequently been included with the Astropectinidae, from which they differ by the presence of an anus, by the large size of the adambulacral ossicles, and by the absence of supra-ambulacral plates. There are four sub-families, including sixteen genera. SUB-FAMILY 1. PARACHASTERINAE, comprising those in which the branchial vesicles or papulae are limited to an area at the base of the rays, and in which the actinal interradial plates are absent or are very few in number. Genera—*Cheiraster*, Studer; *Pararchaster*, Sladen; *Pectinaster*, Perrier; and *Pontaster*, Sladen. SUB-FAMILY 2. PLUTONASTERINAE, including those with papulae scattered over the whole abactinal surface. There are numerous actinal interradial plates. Genera—*Crenaster*, Per. (non Ag.); *Dytaster*, Slad.; *Goniopecten*, Per.; *Lonchotaster*, Slad.; *Persephonaster*, Mason & Alcock; *Plutonaster*, Slad.; *Tethyaster*, Slad. SUB-FAMILY 3. PSEUDARCHASTERINAE, including those with a definite median line of plates along the rays, and with the abactinal plates arranged in series parallel to the central line. There are no pedicellariae. Genera—*Pseudarchaster*, Slad.; *Aphroditaster*, Slad. SUB-FAMILY 4. ARCHASTERINAE, including those in which there is a definite median line of abactinal plates, and the remainder are arranged in oblique rows. Pedicellariae present. Genera—*Acantharchaster*, Verrill; *Archaster*, Verr.; *Isaster*, Verr. The following genera are included by Sladen in this family, but not divided among the sub-families:—*Benthopecten*, Verr.; *Blakiaster*, Per.; *Luidiaster*, Stud.

FAMILY 6. PORCELLANASTERIDAE. Phanerozonia with opposite ambulacral plates; with thin lamelliform marginal plates, traversed by cribriform organs. There are two sub-families. SUB-FAMILY 1. PORCELLANASTERINAE, in which the cribriform organs are highly developed and limited to a few plates, and there are no fimbriated channels in the actinal interradial areas. Genera—*Caulaster*, Per.; *Porcellanaster*, Wyv. Thomson (Fig. VIII.); *Styracaster, Hyphalaster, Thoracaster*, and *Pseudaster*, Sladen. SUB-FAMILY 2. CTENODISCINAE, in which the cribriform organs are simple and occur on the margins of each pair of marginal plates; continuations from the cribriform organs run through the actinal interradial areas as "fimbriated channels." Genus—*Ctenodiscus*, Müller & Troschel. The most interesting features of this family are the development of the cribriform organs, densely packed groups of small spinelets or lamellae on some or all of the marginal plates. Their function is uncertain, but, according to Sladen, "it is not improbable they act as percolators." In some species of *Astropecten* the marginal ossicles are bordered by fringes of small spines, which A. Agassiz has compared to the fascioles of

Spatangoids (see p. 319). In *Ctenodiscus* the grooves between the marginal ossicles are bordered by bands of lamellae forming the simplest type of cribriform organs. In the rest of the Porcellanasteridae these organs are confined to a few special plates. In some species of this family the anus opens on the summit of a small tube. It rises from the abactinal surface of the starfish, and has been accordingly compared to the stem of Crinoids, an homology which is quite inadmissible.

FAMILY 7. ASTROPECTINIDAE. Phanerozonia with opposite ambulacral plates and paxilliform abactinal plates. Super-ambulacral plates are present, and the adambulacral plates are compressed. There is no anus, and pedicellariae are rarely present. The compressed adambulacral plates and the presence of a series of super-ambulacral plates, which occur inside the arms above the ambulacrals, are the two most striking features of the Astropectinidae. The position of the super-ambulacral plates is shown in Fig. VII. There are two sub-families and nine genera. SUB-FAMILY 1. ASTROPECTININAE, including those members of the family in which the adambulacral plates touch the infero-marginal plates along the ray. The marginal and adambulacral plates do not correspond in length or number. Genera — *Astropecten*, Schulze; *Bathybiaster*, Danielssen and Koren; *Craspidaster*, Slad.; *Dipsacaster*, Alcock; *Blakiaster*, Per. (syn. *Leptoptychaster*, Smith), (Fig. IX.); *Moriaster*, *Phoxaster*, and *Psilaster*, Sladen. SUB-FAMILY 2. LUIDIINAE. Astropectinidae with a row of small plates separating the adambulacral and infero-marginal plates. Genera—*Astrella*, Per.; *Luidia*, Forbes; *Platasterias*, Gray.

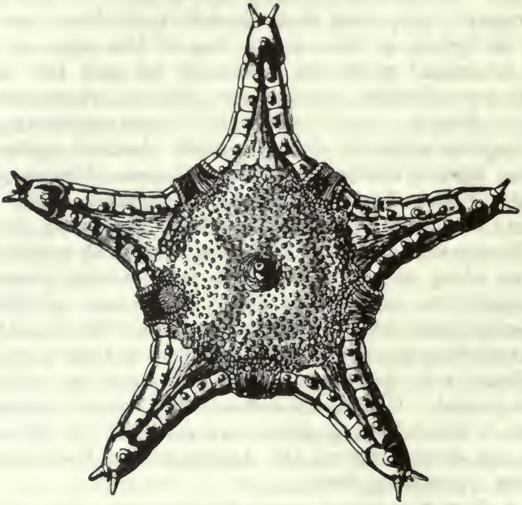


FIG. VIII.

Porcellanaster caeruleus. Abactinal surface showing cribriform organs and anal tube.

FAMILY 8. PENTAGONASTERIDAE. Phanerozonia with opposite ambulacral plates, large marginal plates, and tessellate abactinal skeleton.

The arms are short and the shape of the starfish is generally pentagonal. SUB-FAMILY 1. PENTAGONASTERINAE. Pentagonasteridae with rounded, polygonal, or paxilliform abactinal plates. Genera—*Anthenoides*, Per.; *Asterodon*, Per.; *Astrogonium*, Müller & Troschel; *Calliaster*, Gray; *Calliderma*, Gray; *Chitonaster*, Slad.; *Comptonia*, Gray; *Dorigona*, Gray (*Nymphaster*, Slad.); *Goniodon*, Per.; *Hoplaster*, Per.; *Iconaster*, Slad.; *Leptaster*, Lor.; *Mediaster*, Stimps.; *Metopaster*, Slad.; *Mitelephaster*, Alcock; *Mitraster*, Slad.; *Nectria*, Gray; *Odontaster*, Verr. (*Gnathaster*, Slad.); *Paragonaster*, Slad.; *Pentagonaster*, Schulze; *Phaneraster*, Per.; *Pycnaster*, Slad.; *Rosaster*, Per.; *Stephanaster*, Ayres. SUB-FAMILY 2. GONIODISCINAE. Pentagonasteridae with flat, stellate, abactinal plates. Genera—*Goniodiscus*, Müll. & Trosch.; *Leptogonaster*, Slad. (included by Perrier in Archasteridae); *Stellaster*, Gray; *Ogmaster*, v. Martens. SUB-FAMILY 3. MIMASTERINAE. Pentagonasteridae with small, stellate, paxilliferous abactinal plates. The plates of the actinal intermediate areas imbricate over one another. Genus—*Mimaster*, Slad. *Hoplaster*, Per., is included by Sladen in the Pentagonasteridae, but Perrier places it with *Goniodon*, *Gnathaster*, and *Asterodon*, in a special sub-family of Archasteridae.

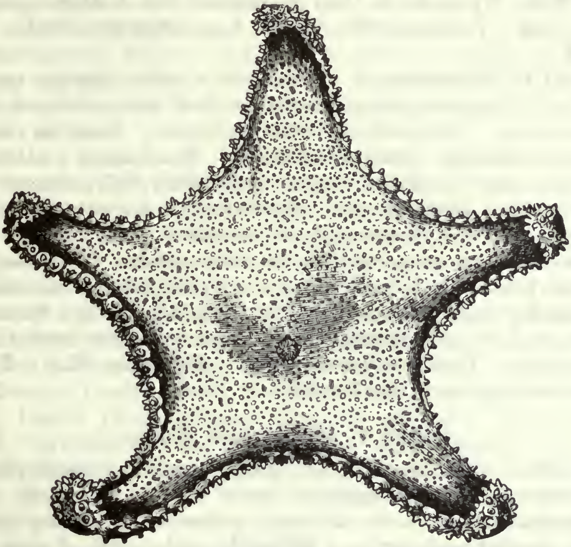


FIG. IX.
Abactinal view of *Hippasterias phrygiana*.

FAMILY 9. ANTHENEIDAE, Per. Phanerozonia with opposite ambulacral ossicles and massive marginal plates. Abactinal skeleton stellato-reticulate; the actinal intermediate plates bear large valvate pedicellariae. Genera—*Anthenea*, Gray; *Goniaster*, Ag. (em. Per.); *Hippasterias*, Gray (Fig. IX.).

FAMILY 10. PENTACEROTIDAE. Phanerozonia with opposite ambulacral ossicles and irregular marginal plates; the upper series are often covered. The abactinal skeleton is reticulate, and the plates bear large tubercles. There are no valvate pedicellariae on the actinal interradial areas. Genera—*Amphiaster*, Verr.; *Asterodiscus*, Gray; *Choriaster*, Lütken; *Culcita*, Ag. (Fig. VI.); *Nidorellia*, Gray; *Paulia*, Gray; *Pentaceropsis*, Slad.; *Pentaceros*, Schulze (*Oreaster*, Müll. & Tr.); *Sphaeraster*, Quenst.; *Sphaerites*, Quenst.

FAMILY 11. GYMNASTERIIDAE. Phanerozonia with opposite ambulacral ossicles and unequally developed marginal plates. Abactinal skeleton tessellate, but its plates are irregular and only partially in contact. The actinal interradial areas contain large plates. The whole test covered with membrane. Genera—*Asteropsis*, Müll. & Tr.; *Dermasterias*, Per.; *Gymnasteria*, Gray; *Lasiaster*, Slad.; *Marginaster*, Per.; *Porania*, Gray; *Poraniomorpha*, Dan. & Kor.; *Rhegaster*, Slad.; *Tylaster*, Dan. & Kor.

FAMILY 12. ASTERINIDAE. Phanerozonia with opposite ambulacral ossicles, and with small, inconspicuous marginal plates, the axes of which are convergent. Intermediate plates imbricate; those on the abactinal side lamelliform. Pedicellaria absent. SUB-FAMILY 1. GANERIINAE, with large marginal plates. Genera—*Cycethra*, Bell; *Ganeria*, Gray; *Lebrunaster*, Per.; *Radiaster*, Per. SUB-FAMILY 2. ASTERINIDAE, in which the marginal plates do not exceed the remaining plates in size. Dermal branchiae arise from any part of the abactinal surface. Genera—*Asterina*, Nardo, which has often been described as a typical Asteroid, and its embryology carefully studied; *Disasterina*, Per.; *Nepanthia*, Gray; *Patiria*, Gray. SUB-FAMILY 3. PALMIPEDINAE, with dermal branchiae confined to the radial regions. Genera—*Palmipes*, Ag.; *Stegmaster*, Slad. *Tremaster*, Verr., is also assigned to this family.

ORDER 2. **Cryptozonia**, Sladen.

Asteroidea with the marginal plates small and inconspicuous or absent; when present the upper and lower rows do not touch. Dermal branchiae not limited to the abactinal surface. Ambulacral plates are generally crowded and narrow. Either the ambulacral or adambulacral plates are the more prominent in the oral skeleton.

This order is characterised by three main characters: (1) The insignificance of the marginal plates, whence the name Cryptozonia; (2) the occurrence of papulae or dermal branchiae beyond the abactinal surface, whence the order is described as "adetopneusic"; and (3) the crowding and narrowness of the ambulacral plates, whence the order is said to be "leptostroterate." The last character is not developed in some Palaeozoic genera that appear to belong to this order.

FAMILY 1. PALAEOCOMIDAE. Cryptozonia with alternate ambulacral ossicles and numerous long free actino-lateral spines. There is a web supported by a reticular calcareous skeleton. The adambulacral plates are large, and the spines are borne on the plates adjoining them. Genus—*Palaeocoma*, Salter. *Bdellacoma*, Salter, is placed by its author as a sub-genus of *Palaeocoma*; its affinities are doubtful, but are certainly not with this family.

Family 2. Lepidasteridae. Cryptozonia with alternately arranged ambulacral ossicles. Disc large; rays comparatively short, thick, and blunt. No lateral spines. The abactinal skeleton consists of closely set, irregular, granular plates. Genus—*Lepidaster*, Forbes (Fig. X.).

Family 3. Tropidasteridae. Cryptozonia with ambulacral ossicles opposite or sub-alternate. Rays short, broad, and flat. Ambulacral ossicles narrow; adambulacral ossicles broad and thin. Abactinal surface granular. Genera—*Tropidaster*, Forbes; (?) *Compsaster*, Worthen & Miller. The name of the type genus was suggested from the apparent occurrence of a keel along the abactinal side of the rays. This, however, is only due to the ambulacral plates being exposed by the loss of part of the granular abactinal integument. *Compsaster* has a narrow ambulacral groove, and is bordered by imbricating actinal plates; its general characters resemble *Tropidaster*, but it is insufficiently known for its affinities to be definitely settled.

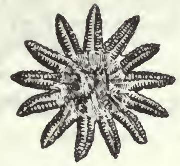


Fig. X.

Lepidaster grayi, Forbes. Wenlock Limestone.

Family 4. Linckiidae. Cryptozonia with opposite ambulacral ossicles, comparatively well-developed marginal plates. Disc small, with long cylindrical rays. Abactinal skeleton tessellate with granular integumentary deposits. Sub-Family 1. Roemerasterinae, with spines on the marginal plates and disconnected granular plates arranged in longitudinal series on the abactinal surface and sides of the arms. Genus—*Roemeraster*, Stürtz. Sub-Family 2. Linckiinae, with abactinal plates devoid of internal supplementary plates. Abactinal and marginal plates granulose and not bearing spines. Genera—*Ferdina*, Gray; *Fromia*, Gray; *Leiaster*, Peters; *Linckia*, Gray; *Narcissia*, Gray; *Nardoa*, Gray; *Ophidiaster*, Ag.; *Pharia*, Gray; *Phataria*, Gray; (?) *Arthraster*, Forbes. Sub-Family 3. Chaetasterinae, with internal supplementary plates and paxilliform tabulae. Genus—*Chaetaster*, Müll. & Tr. In this genus there are remarkable groups of spines borne on the ends of disc-like pillars, rising from the external plates; these are known as paxilliform tabulae. Sub-Family 4. Metrodirinae, with the marginal and abactinal plates covered by membrane. There are neither internal supplementary plates nor paxilliform tabulae. Genus—*Metrodira*, Gray.

Family 5. Stichasteridae. Cryptozonia with opposite ambulacral ossicles and contingent marginal plates. Disc small; rays long and cylindrical. The plates of the abactinal surface are large, closely packed, and regularly arranged. Sub-Family 1. Stichasterinae. The adambulacral plates are equal, have a simple armature, and have no ridges. Genera—*Calycaster*, Per.; *Coelasterias*, Verr.; *Neomorphaster*, Slad.; *Stichaster*, Müll. & Tr.; *Tarsaster*, Slad.; *Tonia*, Gray. Sub-Family 2. Zoroasterinae. The adambulacral plates are unequal, and their armature is complex; alternate plates have ridges. Genera—*Cnemidiaster*, Slad.; *Mammaster*, Per.; *Pholidaster*, Slad.; *Prognaster*, Per.; *Zoroaster*, Wyv. Thoms.

Family 6. Solasteridae. Cryptozonia with opposite ambulacral ossicles, and a reticulate, abactinal skeleton bearing paxilliform groups of spines. Marginal plates obscure. No pedicellariae. Genera—*Crossaster*, Müll. & Tr.; *Ctenaster*, Per.; *Lophaster*, Verr.; *Rhipidaster*, Slad.; *Solaster*, Forbes (Fig. XI.).

Family 7. Korethrasteridae, Dan. & Kor. *Characters*—"Cryptozonia allied to the *Asterinidae*, but distinguished by the complete absence of interbrachial spaces, and by the possession of a continuous, calcareous plating, and the formation of the paxillae" (Bell, 4, p. 23). Genera—*Korethraster*, Wyv. Thoms.; *Peribolaster*, Slad.; *Remaster*, Per.

Family 8. Pterasteridae. "Cryptozonia in which the dorsal ossicles carry a spine crowned by long diverging spines which support a more or less well-developed membrane; this forms a marsupial recess for the young. No actinal intermediate plates, interbrachial septa, or pedicellariae" (Bell, 4, p. 23). In this family the most remarkable feature is the development of a large marsupium in which the young are reared. This is formed by a large veil above the abactinal surface, from which it is raised by numerous long paxillae. The dorsal membrane is perforated by many small pores ("spiracula," Sars), and has a large central opening, the "oscular orifice." In some genera, *e.g. Pteraster*, there are also openings to the actinal surface, known as "segmental apertures." There are often long spines, attached to the rays close by the adambulacral plates; these are known as the actino-lateral spines, and they are either enclosed in the membrane of the actinal surface or in a marginal web. Sub-Family 1. Cheiroptasterinae, with alternate ambulacral ossicles and short actino-lateral spines. (The presence of the marsupium is not certain.) Form

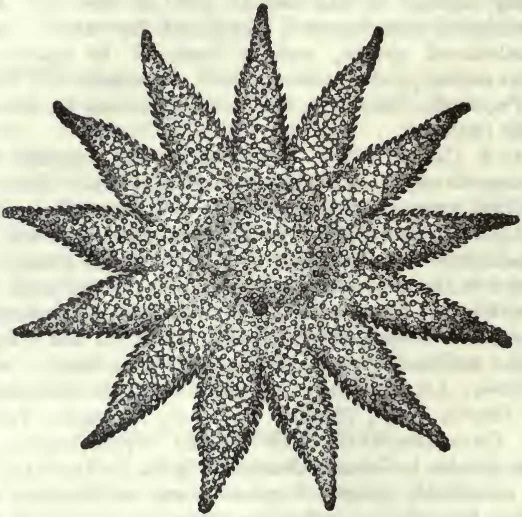


Fig. XI.
Abactinal surface of *Solaster papposus*.

pentagonal. Genera—*Cheiroptaster*, Stürtz; *Loriolaster*, Stürtz; (?) *Rhopalocoma*, Salter. SUB-FAMILY 2. PTERASTERINAE, with a well-developed supra-dorsal membrane, opposite ambulacral plates, and actino-lateral spines. Form pentagonal. Genera—*Benthaster*, Slad.; *Calyptaster*, Slad.; *Cryptaster*, Per.; *Flexaster*, Per.; *Hymenaster*, Wyv. Thoms. (Fig. XII.); *Marsipaster*, Slad.; *Myxaster*, Per.; *Steraster*, Müll. & Tr.; *Retaster*, Per. SUB-FAMILY 3. PYTHONASTERINAE, with stellate form, opposite ambulacral ossicles, and rudimentary marsupium formed by five triangular fan-like valves; no segmental apertures or actino-lateral spines. Genus—*Mayraster*, Per.; *Pythonaster*, Slad.

FAMILY 9. PALASTERISCIDAE. Cryptozonia with the ambulacral ossicles alternate for at least part of the arms. The madreporite is large and ventral in position. Actino-lateral spines are present. The dorsal integument is granular. The form is stellate with small interbrachial areas. Genera—*Palasteriscus*, Stürtz; *Echinasterella*, Stürtz. This family is remarkable for the abnormal position of the madreporite, which, unlike that of recent Asteroids, is ventral in position. This character is possibly due to the development of a granular integument over the whole of the abactinal surface. Large spine-like paxillae occur, and it is quite possible that the granular integument was the roof of a large marsupium. There can be no question as to the position of the madreporite, for the actinal and abactinal surfaces of the same specimen are shown in examples in the British Museum.

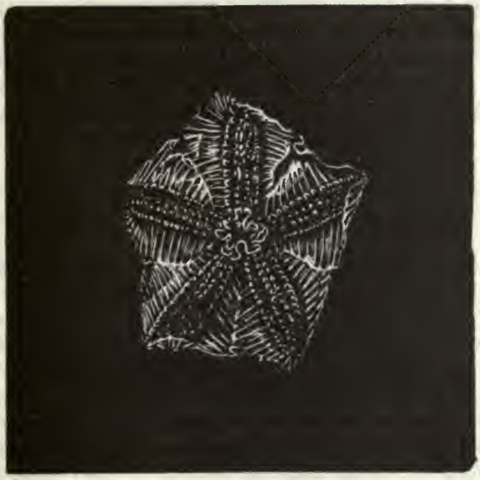


FIG. XII.

Hymenaster pellucidus (after Wyv. Thomson).

FAMILY 10. ECHINASTERIDAE. Cryptozonia with a reticulate abactinal skeleton of small imbricating plates. Ambulacral ossicles opposite; the pores biserial; oral armament adambulacral. Interbrachial septa single if present. SUB-FAMILY 1. ACANTHASTERINAE, with large disc and numerous rays; numerous madreporites. Genus — *Acanthaster*, Gerv. SUB-FAMILY 2. MITHRODIINAE, with a small disc, usually five rays. One madreporite; no interbrachial septa. Armed with large scaly spines. Genus—*Mithrodia*, Gray. SUB-FAMILY 3. ECHINASTERINAE, with a small disc and five or six rays. Spines small and simple. No pedicellariae. Genera—*Dictyaster*, Mason & Alcock; *Echinaster*, Müll. & Tr.; *Henricia*, Gray (syn. *Cribrella*, Ag.); *Perknaster*, Slad.; *Plectaster*, Slad. SUB-FAMILY 4. VALVASTERINAE, with the marginal plates bearing large valvate pedicellariae. The disc is moderate in size, and there are five rays. Genus—*Valvaster*, Per.

FAMILY 11. HELIASTERIDAE. Cryptozonia with opposite ambulacral ossicles and double interbrachial septa. The disc is large and bears very numerous short rays. SUB-FAMILY 1. HELIANTHASTERINAE. The abactinal skeleton is granular in the disc and bases of the arms; at the arm tips it is tessellate, but the plates not in contact. Arms separate at their bases, so that the two sets of plates which form the interbrachial septa are separated by parts of the disc. Infero-marginal plates occur round the disc. Madreporite marginal. Genus—*Helianthaster*, F. Roem. This includes two Devonian species, of which only one is adequately known, and is of somewhat uncertain affinities. It was originally regarded as an Asteroid, but Stürtz, in his latest description of its anatomy, referred it to the Euryalidae. Stürtz's specimens, now in the British Museum, show nothing to separate them from the Asteroidea, of which however they are very abnormal representatives. The ambulacral plates are thin and L-shaped, but not crowded as in *Heliaster*, while the abactinal skeleton is different. The species appears, however, to be a primitive form of the Heliasteridae, in which the arms do not occupy the whole margin of the disc, and are separated from one another throughout; the ambulacral plates are not crowded, so that the podia are biserial. SUB-FAMILY 2. HELIASTERINAE, with reticulate, abactinal skeleton and arms in contact with one another at their bases, there being no interbrachial spaces. The ambulacral ossicles are crowded and the pores quadriserial. Genus — *Heliaster*, Gray.

FAMILY 12. PEDICELLASTERIDAE. Cryptozonia with opposite ambulacral ossicles, a small disc and narrow sub-cylindrical rays. Podia biserial. The abactinal skeleton consists of narrow plates forming a quadrangular network. Genera — *Coronaster*, Per.; *Gastraster*, Per.; *Lytaster*, Per.; *Pedicellaster*, Sars.

FAMILY 13. ASTERIIDAE. Cryptozonia with opposite ambulacral ossicles. Podia quadriserial. Abactinal skeleton reticular and composed of small unequal plates. Genera (including sub-genera of *Asterias*)—*Anasterias*, Per.; *Asterias*, Linn.; *Calvasterias*, Per.; *Coscinasterias*, Verr.; *Cosmasterias*, Slad.; *Diplasterias*, Per.; *Hydrasterias*, Slad.; *Leptasterias*, Verr.; *Podasterias*, Per.; *Polyasterias*, Per.; *Pycnopodia*, Stimps.; *Sclerasterias*, Per.; *Smilasterias*, Slad.; *Sporasterias*, Per.; *Uniophora*, Gray. The anatomy of *Asterias* is described on pp. 241-245.

FAMILY 14. BRISINGIDAE. Cryptozonia with opposite ambulacral ossicles; marginal plates absent or rudimentary. Rays numerous and sharply marked off from the disc. Abactinal skeleton absent, or present only on the ovarial regions at the bases of the arms. No intermediate actinal plates or interbrachial septa. Genera—*Brisinga*, Asbjörnsen; (?) *Brisingaster*, Lor.; *Colpaster*, Slad.; *Freyella*, Slad.; (?) *Gymnobrisinga*, Stud.; (?) *Hymenodiscus*, Per.; *Labidiaster*, Lütken; *Medusaster*, Stürtz; *Odinia*, Per. This remarkable family was originally founded for the genus *Brisinga*, which has many primitive characters. The arms are small and sharply marked off from the disc. There are no ampullae connected to the podia; the generative organs consist of a series of small isolated glands along the arms. The genus was accordingly at first regarded as very primitive in structure and affording in some ways a link with the Ophiuroids. Later authors, however, such as Ludwig and Sladen, entirely repel this view and regard the Brisingidae as allied to the Asteriidae, and extremely specialised rather than primitive. Sladen concludes, "In my opinion the Brisingidae are true cryptozonate Asterids, very nearly related to the Asteriidae, Pedicellasteridae, Heliasteridae, and Echinasteridae, and probably derived from a common ancestor, the divergence of form and the peculiarities of structure now exhibited by *Brisinga* being the result of modification produced by the extreme isolation and the exigencies of the abyssal depths in which the family has existed" (48, p. 593). But in *Colpaster* and *Freyella* the genital glands are limited to swellings at the base of the arms; and although the arms are sharply marked off from the disc, at least six-sevenths of the arm has no extensions of either alimentary canal or generative organs. The arm-ossicles of *Freyella tuberculata* are identical in character with those of *Ophiurina*, and they differ from *Ophiogeron* only by the absence of adambulacral ossicles. Sladen gives no diagnosis of the class Asteroidea, so that it is not quite clear on what characters he would base the separation of Asteroids and Ophiuroids. But no known diagnosis of the Asteroidea would include *Colpaster* and *Freyella*, and exclude forms universally admitted to be Ophiuroids. If the more primitive types of Brisingidae are a recent degenerate offshoot from the Asteriidae or some allied family, then a type of structure, practically indistinguishable from that of the Ophiuroidea, has been twice independently evolved. It seems therefore that Perrier is probably correct when he regards the Brisingidae as the most primitive instead of as the most special of living Asteroids.

The following fossil Asteroids are not sufficiently known for determination:—

Calliaster, Trautschold; *Coelaster*, Sandb. *non* Agass.; *Cribrellites*, Tate; *Cupulaster*, Fritsch; *Plumaster*, Wright; *Trichotaster*, Wright.

SUB-CLASS 2. OPHIUROIDEA.

The Ophiuroidea form a sub-class of the Stelleroidea, including the sand-stars, brittle stars, and branching stars. The typical members of the class differ from the typical Asteroids by having the arms sharply marked off from the disc as appendages, and by not having a groove along the ventral side of the arms. These differences are so important, anatomically, that the Ophiuroidea and Asteroidea are often regarded as distinct classes. Owing to the general external resemblance between the two groups, the first naturalists who described them made no attempt to separate them. Thus Linck, who in 1733 (23) figured several Ophiuroids, included most of them, along with some Asteroids, in his genus *Stella*. The common British species, *Ophiura ciliaris*, Linn. sp., he named *Stella lacertosa*, and *Ophioderma longicauda* he described as *Stella lumbricalis longicauda*. He, however, recognised that his group "Stella" must be broken up into several divisions, for he separated *Ophiothrix fragilis*, O. F. Müller sp., under the name of *Rosula*, and the branching forms under the name of *Astrophyton*. Linnaeus, on the other hand, did not grant the Ophiuroids even generic distinction, and included them all in the genus *Asterias*. It was not until 1816 that Lamarck (21) definitely founded the genera *Ophiura* and *Euryale*. De Blainville in 1834, L. Agassiz in 1836, Dujardin in 1840, and Müller and Troschel in 1844, added greatly to the systematic knowledge of the Ophiuroids, which they retained in the order Stellerida. The first proposal to separate the group as one of the primary divisions of the Echinoderms was made by Forbes in 1840 (11); he founded the order "Spinigrada" for the Ophiuroids, while the Asteroids he named the "Cirrigrada." Gray, in 1840 and 1848, kept the two groups as separate orders, but united them in one class, Hypostoma. Since this date the view that the Ophiuroids are a distinct class has been widely adopted.

The sub-class includes over one hundred genera, most of which are recent. The earliest fossil forms occur in the Ordovician, and representatives are known from all later systems.

The recent species have been described by many authors, especially by Bell, Düben, Forbes, Grieg, Grube, Heller, de Loriol le Fort, Ljungman, Lütken, Lyman, Marenzeller, v. Martens, Mortensen, J. Müller, W. Peters, G. O. Sars, Sladen, Stimpson, Studer, and Verrill. Lyman's report on the *Challenger* Collection is a complete synopsis up to 1882 (31).

The fossil Ophiuroids are rare, and, as a rule, badly preserved. The literature consists mainly of the description of isolated specimens, as by E. Billings, Böhm, Forbes, S. A. Miller, Pohlig, C. F. Roemer, H. Woodward, Worthen, and Wright. Stürtz and Roemer have described the remarkable fauna from Bundenbach in Germany, and Salter that from the English Silurian. References to the American Palaeozoic species are given in Miller's *North American Geology and Paleontology*.

The first classifications of the Ophiuroids were artificial; the basis of a natural arrangement was laid by Ljungman in 1867 (24). Previous to that date the group had been divided into two families—the Ophiuridae, including the forms with simple arms, and the Astrophytidae, the members of which have branched arms. Raised to sub-orders and divided into families, these two divisions have long survived. In 1892 Bell (3) proposed a classification into three orders, to which a fourth has been added to include some fossil forms (Gregory, 15).

The first important contributions to the anatomy of the Ophiuroids were an account of the structure of the Euryaleae by L. Agassiz, and of the skeleton of various genera by Müller (1854). Further researches have been carried out by Cuénot (1888) and Hamann (1889). The two authors, however, to whom we are most indebted are Lyman, who, in a long series of papers, has described the skeletal structures, and Ludwig, whose masterly memoirs gave the first detailed account of the visceral anatomy. Genera of exceptional interest have been described by Bell, Ludwig, Simroth, and Sladen, to whom we owe memoirs respectively, on *Ophioteresis*, *Trichaster*, *Ophiactis*, and *Astrophiura*. The development was first studied by Müller and Krohn (1851); Ludwig in several memoirs, and Apostolides (1882), Russo (1891), Cuénot (1892), and Bury, have studied additional forms with modern methods; while MacBride, in 1896, has shaken, if not destroyed, faith in the theory of the homology of the "calycinal" plates (p. 14) as taught by Lovén, Carpenter, and Sladen.

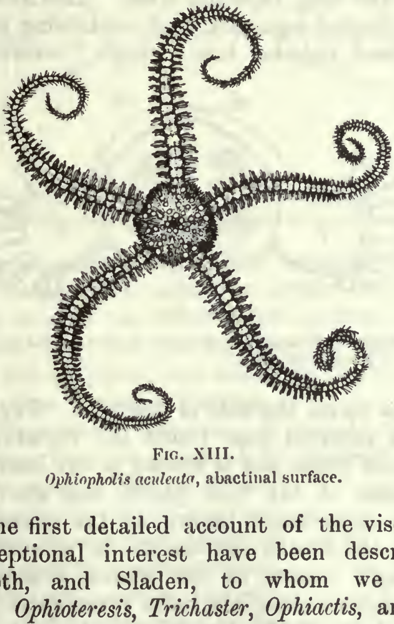


FIG. XIII.
Ophiopholis aculeata, abactinal surface.

The body of an Ophiuroid, like that of an Asteroid, consists of a central disc, from which radiate several (generally five) arms (Fig. XIII.). The disc, however, is not formed, as it is in Asteroids, by the union of the bases of the arms, but is sharply marked off from them, and they are attached to it as appendages; there is not, moreover, in the Ophiuroids the ventral groove of the starfish. These characters, however, are not absolutely to be relied on; thus in some species of *Astroschema* there is no sharp separation between the arms and the disc; while in *Ophioteresis* (Fig. XIV.) the radial ambulacral vessels and nerve-trunks lie in shallow grooves on the ventral surface of the arms.

An idea of the **Structure of a typical Ophiuroid** may probably be best obtained by the careful examination of a representative species, for which purpose the commonest English brittle star (*Ophiura ciliaris*, Linn. sp.) is a convenient type.

This Ophiuroid consists of a round, flat, scale-covered disc, from which radiate five long, tapering arms. The Arms are composed of a series of jointed segments, each containing six plates. Two of these are fused together into a single "vertebral ossicle," and a series of these forms the axis of the arm. The remaining four plates form an external tube round the vertebral ossicle. One pair occurs at the sides, and is known as the lateral arm-plates or shields. Another of the four plates lies above the vertebral ossicle, and is accordingly known as the dorsal arm-plate (or dorsal shield); the fourth lies on the lower surface of the arm, and is accordingly known as the ventral arm-plate (or ventral shield). Each lateral arm-plate bears seven short spines.

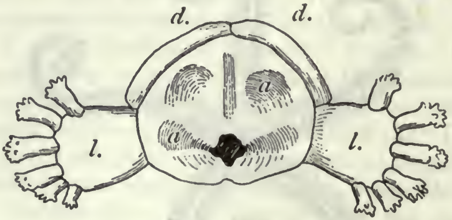
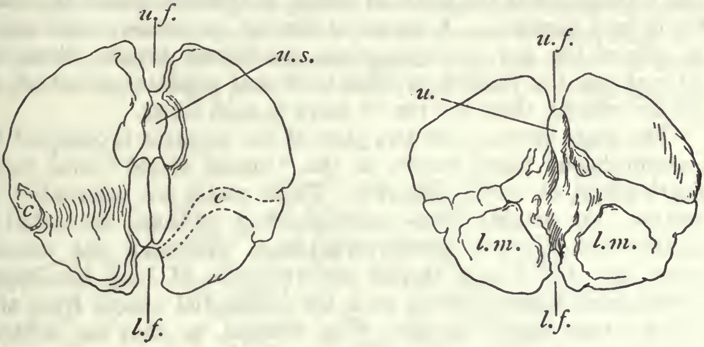


FIG. XIV.

Ophioteresis (after Bell). Aboral surface of an arm ossicle; *d*, the double dorsal arm-plates; *a*, articular cavities; *l*, lateral arm-plates.

The plates forming the central chain of the arm are known as "vertebral ossicles," because, in typical Ophiuroids such as *Ophiura ciliaris*, they articulate by a series of knobs and sockets like the bones of a vertebral column. In a typical vertebral ossicle the two articular surfaces are very different; in the proximal or adoral surface (that nearer to the disc) the most conspicuous features are the prominent central umbo (Fig. XV. *u*) and two broad "lower muscle fields" (Fig. XV. *l.m*) at the two lower angles. Above the umbo there is a narrow "upper canal furrow" (*u.f*), while a corresponding "lower canal furrow" (*l.f*) occurs between the two muscle fields. Above the lower furrow there is a depression to receive a prominence on the distal face of the adjoining ossicle, and on each side of the depression there is small knob, which similarly fits into depressions on the adjacent ossicle. On the distal or aboral surface there is a deep "umbonal socket" (*u.s*), and also the prominence and two hollows already referred to; the two lower angles are occupied by broad expanded surfaces, under which pass the tubes of the podia (the surface on one side in figure is broken away to show the canal for the podion, *c*).



1. 2.

Fig. XV.

Vertebral ossicle of *Ophiura ciliaris* (after Müller). 1, aboral surface; 2, adoral surface. *u*, umbo; *l.m*, lower muscle field; *u.f*, upper, and *l.f*, lower canal furrows; *u.s*, umbonal socket; *c*, canal for the podion (shown by removal of part of muscle field on right side).

Passing from the arms to the Disc, the skeleton is seen to consist of two sets of plates, one belonging to the external integument, and the other to the oral system.

The Oral Skeleton is complex. It may be most readily conceived as resulting from the fusion of the elements of two segments in each of the arms. The entire oral skeleton surrounds the mouth, and consists of as many segments as there are arms. Each segment is roughly triangular in shape, the apex pointing inwards, and being separated by the deep "buccal fissures." The principal element in each segment is a pair of "syngnaths" (Fig. XVI.), also known as oral angle-plates, jaws, mouth-plates, *scutella oralia*, etc.; the name syngnath is suggested for them, as they consist of two parts generally completely fused together. The larger piece of the syngnath is the mouth frame (*m.f*), which unites with the corresponding plate of the next segment across the buccal

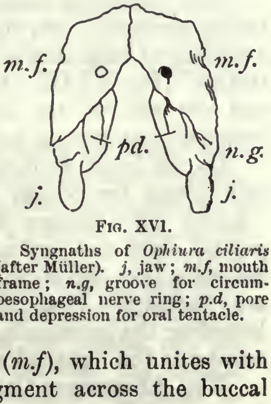


Fig. XVI.

Syngnaths of *Ophiura ciliaris* (after Müller). *j*, jaw; *m.f*, mouth frame; *n.g*, groove for circumoesophageal nerve ring; *p.d*, pore and depression for oral tentacle.

fissure. The smaller piece is the jaw, which unites with the jaw of the next arm to form the angle of the oral segment. Each jaw has a depression, in which rest the oral tube-feet, and is notched by a groove for the circumoral nerve ring.

The union of two adjoining jaws is strengthened by a small plate at the apex, known as the "jaw plate" or *torus angularis.* This plate supports the teeth, of which, in *Ophiura ciliaris*, there are five in each segment. A series of similar processes occur along the side of the jaw, projecting into the buccal fissure; these are the oral papillae (mouth papillae or buccal papillae), of which, in *Ophiura ciliaris*, there are ten or more in each series.

The angle between the two jaws of one segment is occupied by a shield-shaped plate, known as the "buccal shield" (oral plate, mouth-shield, or *scutum buccale*). These plates are interradial in position; the smaller plates corresponding to them, but radial in position, are the first ventral arm-plates. Between the mouth-frames and the buccal shields are five pairs of long, bar-shaped "peristomial plates," which cross the interradial spaces from arm to arm; they cannot be seen from without, as they are covered by the shields, and by two plates beside the latter, known as the lateral buccal shields (or *scuta adoralia*).

The oral skeleton of the Ophiuroid is therefore very different from that of the Asteroid. But both are formed by the modification of similar parts, viz. the ambulacral and adambulacral ossicles of the arm segments. In the Ophiuroid the supposed homologies of the principal parts are as follows:—

	Vertebral (=ambulacral ossicles).	Lateral arm-plates (=adambulacral ossicles).
1st arm segment	peristomial plates	jaws
2nd ,,	mouth-frames	lateral buccal shields.

The remaining elements in the skeleton of *Ophiura* belong to the exoskeleton. On the upper or aboral side of the disc there are five pairs of large and somewhat pyriform plates known as "radial shields" (Fig. XXIII. *r.s*). Between them are a few smaller plates, and the rest of the disc of *O. ciliaris* is covered with small, irregular, imbricating scales.

On the lower surface of the disc there are two pairs of long, thin plates beside the bases of the arms. A narrow cleft, the "bursal slit" (known also as the bursal aperture, genital slit, genital cleft, and ovarian aperture), separates these plates. This slit leads into the bursal cavity, into which the generative products are discharged from the gonads. Of the two bar-like plates bounding the bursal slit, the larger is the "genital plate," and the smaller is the "genital scale."

The Alimentary Canal of the Ophiuroids is simpler than in either Asteroids or Echinoids. The mouth is situated in the centre of the lower surface of the disc, and from it the buccal fissures radiate. The mouth opens to a short oesophagus, above which is a large digestive sac, occupying nearly the whole cavity of the disc. Neither anus nor diverticula along the arms are present.

The Water-vascular System consists essentially of a circumoesophageal ring which gives rise to five radial vessels bearing tube-feet, and five vesicles, one of which communicates with the exterior. In *Ophiura ciliaris* the circumoesophageal ring lies over the syngnaths, through which pass branches (Fig. XVII. *o.v*) leading to the mouth-tentacles (*o.t*); radial vessels run along the under sides of the arms. In each of four of the interradial (or interbrachial) spaces there is a "polian vesicle" (*p.v*); in the fifth interradius there is a short expanded stone-canal (Fig. XVIII. *s.c*) which opens to the exterior by a single madreporite on a buccal shield. The radial vessels lie in the lower canal furrows of the vertebral ossicles (Fig. XV. *l.f*); branches from the radial vessel pass through the vertebral ossicles; they emerge at the lower angle of the ossicle, and the podia pass to the exterior through a space between the shields. There are no ampullae, but the flow of water is regulated by

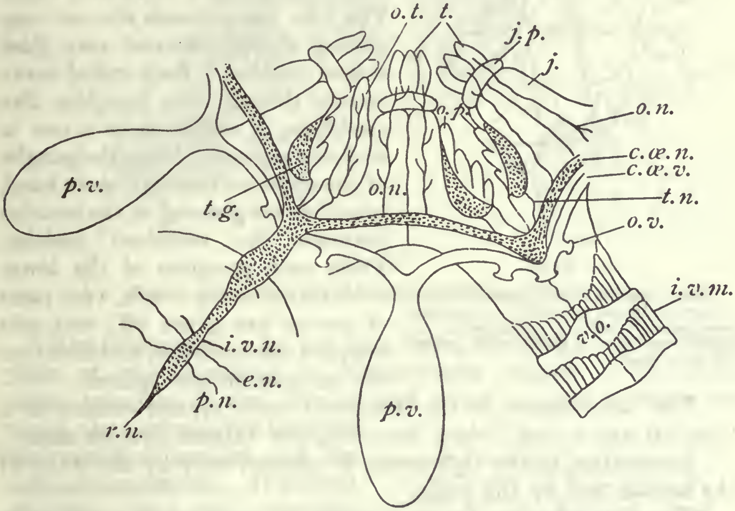


FIG. XVII.

Diagram of circumoral region of *Ophiura ciliaris* (after Müller). *c.œ.n*, circumoesophageal nerve ring; *c.œ.v*, circumoesophageal water-vascular ring; *e.n*, nerve branch to integument; *i.v.m*, intervertebral muscles; *i.v.n*, intervertebral nerve; *j*, jaw; *j.p*, jaw plate; *o.n*, oral nerve; *o.p*, oral papillae; *o.t*, oral tentacle; *o.v*, branch of water vessel to oral tentacle; *p.n*, podial nerve; *p.v*, Polian vesicle; *r.n*, radial nerve; *t*, teeth; *t.g*, tentacular groove; *t.n*, tentacular nerve; *v.o*, vertebral ossicles.

valves. There are no suckers, so the podia are useless in locomotion.

The Nervous System of *Ophiura ciliaris* consists of a circumoesophageal ring, from which radiate five radial nerve trunks (Fig. XVII. *c.œ.n* and *r.n*); it also gives off small branches to the oral tentacles, teeth, and oral muscles. The radial nerve trunks consist of two separate nerve bands, one above the other, both lying in the "epineural canal" (Fig. XXI. *e.r.n* and *i.r.n*). The two nerve bands are not connected, though situated very close to one another. Both radial nerve trunks thicken into ganglion-like swellings, of which there is one in each arm segment. From the ganglia of the upper or internal nerve band, branches are given off to the muscles between the vertebral ossicles. From each ganglion of the lower or external nerve trunk, two pairs of nerves are given off; one pair supplies the tentacles, and the other the integument and spines.

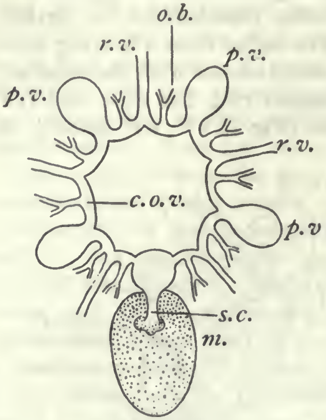


Fig. XVIII.

Water-vascular ring of *Ophiura ciliaris*. *o.b*, branch to oral tentacles; *c.o.v*, circum-oesophageal vessel; *m*, madreporite; *p.v*, polian vesicle; *r.v*, radial water vessel; *s.c*, stone canal.

The last element in the Ophiuroid nerve system consists of a "genital nerve ring," which lies along the "aboral circular sinus."

Respiration in the Ophiuroids is effected only by the walls of the bursae, and by the podia.

The Reproductive Organs consist of a series of small pear-shaped gonads (Fig. XIX. *g*) which do not open directly to the exterior, but into the bursae, where, in some cases, the development takes place. In *Ophiura* there are more than forty gonads to each bursa.

The Coelomic Sinus. There appears to be no true blood-vascular system in the Ophiuroids; the vessels which have been described as such are connected with the axial sinus, and are therefore coelomic spaces and not vessels (MacBride, 32, and Russo). The axial sinus (Fig. XX. *x.s*) is the most important; it is the space through which runs the stone-canal, and it contains a gland in contact with the stone-canal, which is known as the "ovoid gland" or "axial organ" (*x.o*), (see p. 23). From the upper end of the axial canal runs the "aboral circular sinus." The course of this sinus is very sinuous: above the arms it is aboral in position, but beside the arms it bends downwards until, in the interradii, it is quite ventral in position. The main sinus passes on the interradial side of the bursae, and sends off a branch along the radial side of each bursa. The parts of the sinus beside the bursae bear the gonads.

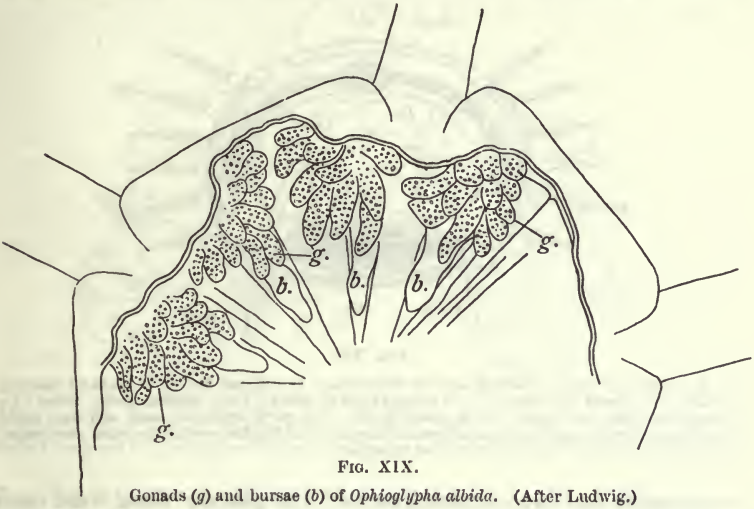


Fig. XIX.

Gonads (*g*) and bursae (*b*) of *Ophioglypha albida*. (After Ludwig.)

Arm Structure. As we have seen, there are no prolongations of the digestive or reproductive organs in the arms, while branches of the nervous and water-vascular systems run along the ventral side between the vertebral ossicles and the ventral arm-shields. It follows therefore that the vertebral ossicles are directly supra-ambulacral, and are homologous with the ambulacral ossicles, and not with the supra-ambulacral ossicles of such Asteroids as *Astropecten*. A transverse section across an Ophiuroid arm is shown in Fig. XXI. (cf. p. 15).

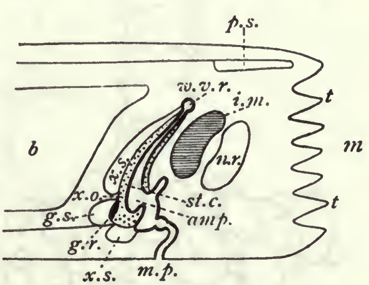


Fig. XX.

Diagrammatic section through oral region of Ophiuroid (after MacBride). *amp*, ampulla ; *b*, bursa ; *i.m*, interradial muscle of the disc ; *g.s*, genital sinus ; *g.r*, genital rhachis ; *m*, mouth ; *m.p*, madreporic pore ; *n.r*, circumoesophageal nerve ring ; *p.s*, peristomal sinus ; *st.c*, stone canal ; *t*, teeth ; *w.v.r*, water-vascular ring ; *x.o*, axial organ ; *x.s*, axial sinus.

From such a type as *Ophiura ciliaris*, with its smooth, flat, circular disc, its irregular, scaly plates, its comparatively short, straight, unbranched, and regularly tapering arms, there are many striking deviations, both in aspect and structure.

The Exoskeleton may be either more or less complete than in

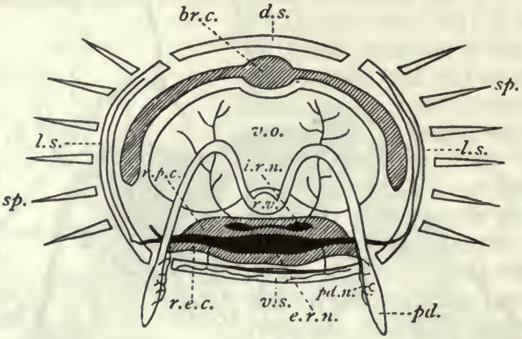


Fig. XXI.

Diagrammatic section through arm of Ophiuroid. *br.c*, **dorsal branch of brachial coelomic system**; *d.s*, dorsal arm-plate; *e.r.n*, external radial nerve; *i.r.n*, internal radial nerve; *l.s*, lateral arm-plate; *pd*, podion; *pd.n*, podial nerve; *r.e.c*, radial epineural canal, and *r.p.c*, radial pseudhaemal canal, together forming ventral branch of the brachial coelomic system; *r.v*, radial vessel; *v.o*, vertebral ossicle; *v.s*, ventral arm-plate.

Ophiura. The most important addition to the plates found in that genus is formed by the plates of the so-called "apical system." In some species, such as *Ophiomusium validum*, there is a central plate surrounded by three circlets, each of five plates; these were once regarded as homologous with plates in Asteroids and Crinoids, and therefore named the infra-basals, basals, and radials. In some species, such as *Ophiomitra exigua*, the two circlets of radially situated plates are absent, and only the central and basal plates are present. In *Ophiocrene* and *Ophiura convexa*, Lym. sp., there are only the central plate and the radials; in *Ophiura minuta*, Lym. sp., there are the central, radial, and basal plates. The last possible combination occurs in a species of *Pectinura* (Fig. XXII.), in which the two circles of plates round the central have been described as the radials and infra-basals. In some other forms, such as *Ophioceramis obstricta*, Lym. (Fig. XXIII.), there is a remarkable uniformity in the plates on the dorsal aspect, but these are not arranged on the calicular plan. In some other cases, such as *Ophiura inornata*, Lam. sp. (Fig. XXIV.), there are two "infra-basal" plates side by side

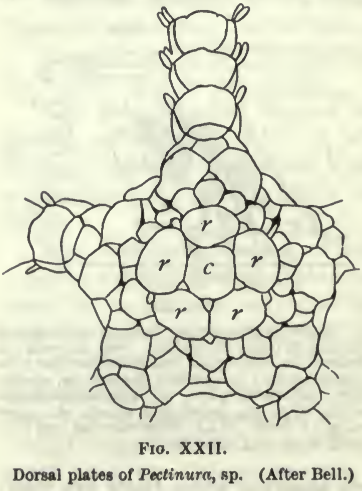


Fig. XXII.

Dorsal plates of *Pectinura*, sp. (After Bell.)

below each radial. The genus in which these supposed calycinal plates most resemble a Crinoid cup is the genus *Ophiopyrgus*

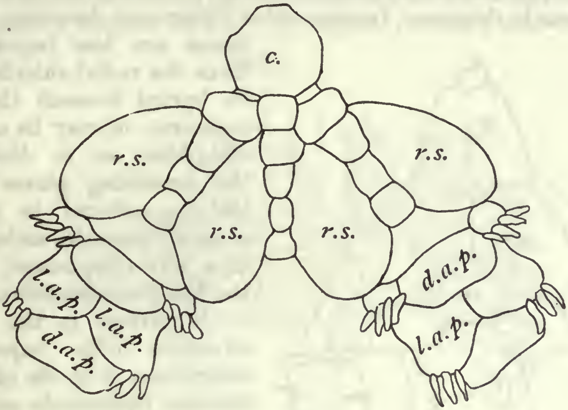


Fig. XXIII.

Abactinal plates of *Ophioceramis obstricta*, Lym. (after Lyman). *c*, central plate; *r.s*, radial shields; *d.a.p* and *l.a.p*, dorsal and lateral arm-plates.

(Fig. XXV.), in which the dorsal side is raised into a conical projection.

The irregularity of these "calycinal plates" both in development and arrangement discredits their supposed homology with the three circlets of plates in the calyx of a Crinoid. It is only natural that among the many variations in the grouping of the

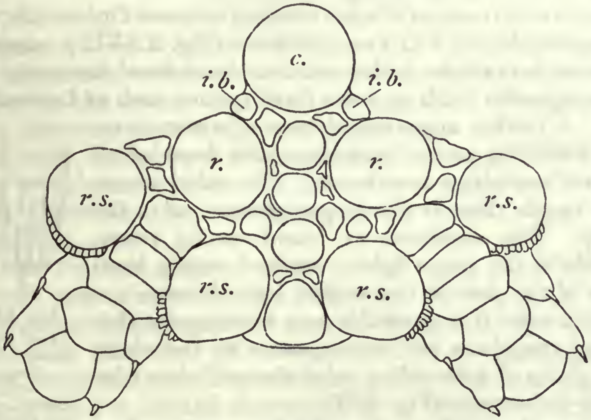


Fig. XXIV.

Abactinal plates of disc of *Ophiura inornata* (Lam.). *c*, central, *r.s*, radial shields.

dorsal plates of Ophiuroids, that one or more pentamerous rings should be more conspicuous than the rest.

In the previous cases the dorsal plates of the disc are more prominent than in *Ophiura*. In some other Ophiuroids, however, these plates are less important. Thus the radial shields may be buried beneath the integument, or may be absent altogether, as in *Neoplax;* the remaining plates may also be reduced to scales or small granules embedded in a soft integument, as in the Gorgonocephalidae.

Variations in the Arm structure offer important indications as to the affinity between Ophiuroids and Asteroids. The differences between such types as *Ophiura* and *Asterias* are very great; but many intermediate stages occur between these extremes; and in the case of some extinct genera it is doubtful to which sub-class they belong.

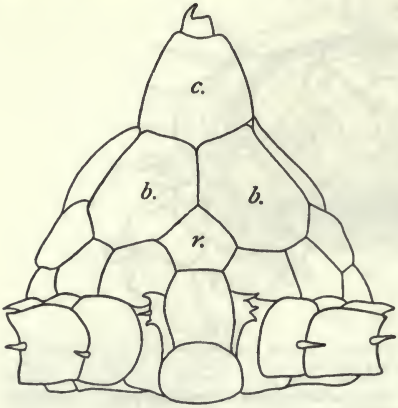


Fig. XXV.

Ophiopyrgus, seen from the side (after Lyman). *c*, central, *b*, basal, *r*, radial plates.

The vertebral ossicles of some existing deep-sea Ophiuroids, such as *Ophiogeron* (Fig. XXVI.) or *Ophiohelus* (Fig. XXVII.), consist of two separate bars similar to the ambulacral ossicles of Asteroids. The same arrangement holds in some fossil species, such as *Lapworthura Miltoni.* A further approximation to the arm structure of Asteroids occurs in some genera from which the ventral arm-plates are absent. The radial water-vascular vessels then lie along open grooves, as in the Asteroids. This condition is found among recent Ophiuroids in the genus *Ophioteresis*, and among fossil members of the class in the extinct Lysophiurae.

In such cases it is generally easy to recognise that the lateral arm-plates are homologous with the adambulacral plates of Asteroids, a point also well shown by the living *Ophioteresis* (Fig. XIV.)

The lateral arm-plates, though often smaller than the ventral or dorsal arm-plates, are morphologically the most important. They are always present, except when the arm is covered by a soft or granular integument, as in the Cladophiurae and some genera of Streptophiurae.

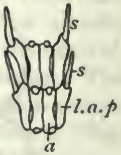


Fig. XXVI.

Arm-plates of *Ophiogeron supinus* (magnified). *a*, ambulacral plate; *l.a.p*, lateral arm-plates; *s*, spine.

The dorsal arm-plates vary more than either of the other sets.

They are double in *Ophioteresis* and *Ophiomyxa pentagona*, are split up into several pieces in *Astroschema* (Fig. XXVIII.), and into a mosaic of small plates in *Hemieuryale ;* or they are absent altogether from many genera, such as *Neoplax*, *Ophiobyrsa*, *Protaster*, *Lapworthura*.

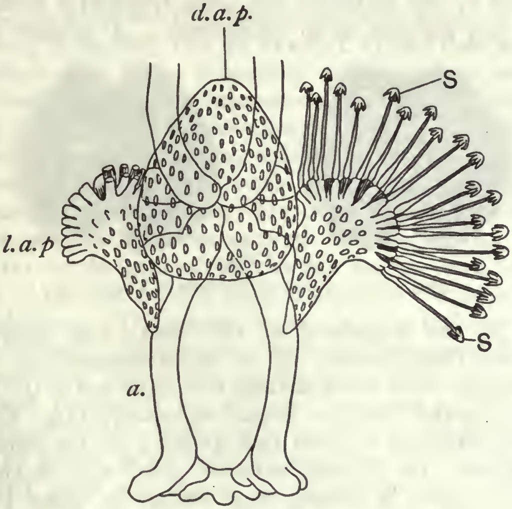


FIG. XXVII.

Arm-plates of *Ophiohelus umbrella*. *l.a.p*, lateral arm-plates ; *d.a.p*, dorsal arm-plates ; *a*, ambulacral plate ; *s*, spines.

Another character by which the recent Asteroids and Ophiuroids differ is the alternation of the ambulacral ossicles in the former, whereas in the latter the pairs are opposite. The Palaeozoic genera, however, also bridge this gap, as in the order Lysophiurae the ambulacral ossicles are alternate as in the Asteroids. This is shown in the arm structure of *Palaeophiura*.

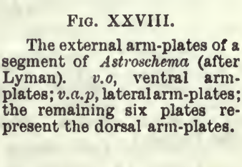


FIG. XXVIII.

The external arm-plates of a segment of *Astroschema* (after Lyman). *v.o*, ventral arm-plates; *v.a.p*, lateral arm-plates; the remaining six plates represent the dorsal arm-plates.

While *Protaster* and its allies on the one hand approximate to the Asteroids, another group of Ophiuroids has arms which appear more like those of Crinoids. In *Ophiura* the arms are fairly straight and only capable of a limited movement in a horizontal plane, for the vertebral ossicles are "zygospondyline," *i.e.* are attached to one another by a series of knobs, closely fitting into sockets (*e.g.* Fig. XV.) In the group of the Streptophiurae much more play of the arms is possible, as the ossicles are "streptospondyline," *i.e.* articulate by simple ball-and-socket joints, without lateral pits and processes (Fig. XIV.); while in the Cladophiurae the ossicles articulate by hour-glass shaped surfaces (Fig. XXIX.), and the four external shields are replaced by a soft, granular integument; in this group the arms are therefore capable of movement in any direction, the arms frequently being able to coil round any support, as in *Astroschema*. A further change is introduced by the branching of the arms; this occurs in two groups of the Cladophiurae, viz. in the Trichasteridae, in which the arms branch a few times at their free ends, and in the Gorgonocephalidae, in which the arms branch repeatedly (Fig. XXXII.).

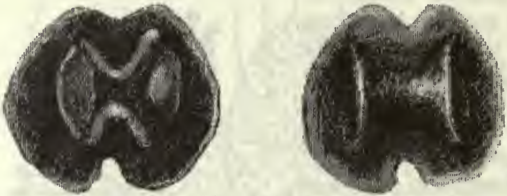


FIG. XXIX.
Articular surfaces of vertebral ossicles of *Astroschema*.

The Oral Skeleton of most Ophiuroids is on the same plan as that of *Ophiura;* the details however differ considerably. The nature of the parts is shown very clearly in some Palaeozoic genera, such as *Sturtzura*. The apparatus here consists of a syngnath, apparently composed of the plates of only a single arm segment; one of the plates of the central vertebral pair is elongated to a bar, and forms the mouth-frame, which is therefore clearly ambulacral. The jaw plate attached to this mouth-frame is the adambulacral plate of the same segment, while the teeth upon this are homologous with spines.

In many recent Ophiuroids there is an element in the armature in addition to those of *Ophiura;* this is the set of "dental papillae" which are situated at the oral ends of the jaws and project toward the mouth above the teeth.

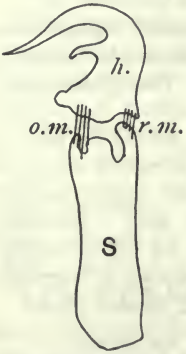


FIG. XXX.
Pedicellaria of *Trichaster elegans*. *h*, hook; *s*, stem; *o.m*, *r.m*, occlusor and retractor muscles. (After Ludwig.)

In *Ophiura* and its allies there are no Pedicellariae, but a very primitive type of them occurs in the Cladophiurae, as in *Trichaster* (Fig. XXX.).

Turning to the internal anatomy we find the most important changes in connection with the Water-vascular System. In many genera of the Cladophiurae there is more than one madeprorite, of which there may be one in each interradius. In

Trichaster the stone-canals are thus repeated, but there is only one madreporite. A repetition of the stone-canals also occurs in *Ophiactis*, in which the value of this character is apparent, for the animal reproduces by fission; in the same genus there are also several Polian vesicles in each interbrachial space. In development the water-pore of recent Ophiuroids originally opens on the dorsal surface (Bury, 6, pp. 422, 423, pl. xxxvii. f. 2), and then works round to the ventral side, where it becomes attached to an oral plate.

The Alimentary System remains very simple in all the Ophiuroids, consisting simply of a large chamber, divided into a series of short, blunt, sac-like protuberances by radial constrictions of the walls.

Respiration in the Ophiuroids is generally effected by the genital bursae and the podia; but when the bursae are absent, their place may be taken by an extra series of Polian vesicles, as in *Ophiactis;* or the general body-cavity may be used both for the protection of the ova and for respiration, as in *Gorgonocephalus.*

Reproduction.—The genital bursae in some Ophiuroids also act as brood chambers; the eggs pass through all stages of development in them, and such Ophiuroids are therefore viviparous; *Amphiura squamata* and *Ophiomyxa vivipara* are examples of this condition. Asexual reproduction occasionally occurs in Ophiuroids either normally by fission, as in *Ophiactis*, or abnormally by regeneration of lost parts when the disc of an Ophiuroid is cut into halves. Broken arms are readily replaced, but a broken arm cannot reproduce a complete animal as can be done in the Asteroids (Semon and Ludwig).

The Development of the Ophiuroids agrees in the early stages with that of the Asteroids, but the larval form is a *Pluteus* (p. 6) and not a Bipinnaria (p. 5). It, therefore, in this stage offers a greater resemblance to the larvae of the Echinoids than of the Asteroids. There is no doubt, however, that this larval form is a secondary development and does not represent any stage in phylogeny of the group; it therefore does not indicate any affinity with the Echinoids.

Distribution.—The Ophiuroids range from shallow and estuarine waters to abyssal depths. Their distribution in space is wide, species such as *Ophiocten sericeum* occurring at 80° N. latitude; but the largest forms are tropical. The order was first represented by species of *Protaster* from Ordovician rocks. Representatives of the Lysophiurae and Streptophiurae occur in the Silurian, Devonian, and Carboniferous strata; Zygophiurae begin in the Trias; and Cladophiurae in the Jurassic.

On the characters discussed in the preceding pages may be based the following **Diagnosis of the Sub-Class:** [1]—The Ophiuroidea are "eleutherozoic," "actinogonidial," and "lysactinic," Echinoderms which usually have no ambulacral groove. The arms are generally sharply marked off from the disc, are generally five in number, and are sometimes elaborately branched. The digestive system, which is aproctous, and the generative system are both confined to the disc; so also is the special respiratory apparatus which takes the form of deep clefts.

---

[1] Emended from Bell (4), p. 215. The terms are explained *antea*, p. 237.

This diagnosis at once indicates that the Ophiuroids are more nearly allied to the Asteroids than to other Echinoderms, for both classes are actinogonidial, eleutherozoic, and lysactinic. Moreover, neither of the main characters which separate the two classes hold in all cases; for in *Ophioteresis* and *Protaster* there is a ventral groove, and in some species of *Astroschema* the arms pass gradually into the disc. Similarly the Asteroids of the family Astropectinidae have no anus; and the Ophiuroids, *Gorgonocephalus* and *Ophiactis*, have no genital bursae.

ORDER 1. **Lysophiurae**, Gregory (1897).

Ophiuroidea in which the ambulacral ossicles are alternate, and are not united into vertebral ossicles, but those of each segment are separate. There are no ventral arm-plates, and the ventral side of the arm is occupied by an ambulacral furrow.

This order includes a group of fossil Ophiuroids, in which the arm structure is asteroid in plan, for there are no ventral arm-plates; there is an ambulacral groove; and the ambulacral plates are in alternate pairs. The members of the order differ from the Asteroids by having the arms sharply marked off from the disc, and the alimentary canal was doubtless confined entirely to the disc.

FAMILY 1. PROTASTERIDAE. Lysophiurae with boot-shaped ambulacral ossicles, each composed of a "body" in the median line of the arm, and a lateral "wing" at right angles to it. Genera—*Protaster*, Forbes, and *Bundenbachia*, Stürtz. There is a well-marked scale-covered disc and five flexible arms. The axial portion or "body" of each ambulacral ossicle is marked off into two parts by a depression which probably served for the attachment of powerful ventral muscles. Stout adambulacral plates occur in all the members of the family, and support lateral spines.

FAMILY 2. PALAEOPHIURIDAE. Lysophiurae in which the ambulacral ossicles consist of a bar-shaped or subquadrate "body" without wings. Genera—*Sturtzura*, Greg.; *Eugaster*, Hall; *Ptilonaster*, Hall; *Taeniura*, Greg.; all Silurian; and the Devonian *Palaeophiura*, Stürtz. This family is characterised by its alternate rod-shaped ambulacral ossicles, shown in *Palaeophiura lymani*, Stürtz.

ORDER 2. **Streptophiurae**, Bell (1892).

Ophiuroidea in which the ambulacral ossicles are opposite, and generally united to form vertebral ossicles. In such cases the vertebral ossicles articulate with one another by means of a more or less simple ball-and-socket joint. The covering plates are more or less regularly developed as superior, inferior, and two lateral, the last of which bear spines.

The diagnosis of this order is necessarily vague, as it includes a series of simple forms, among which there are great divergences in structure. One living genus included in this order has no ventral arm-plates, but a small ambulacral furrow, and thus agrees with the Palaeozoic genera, for which Stürtz in 1885 proposed the family Ophioencrinasteriae. The main character of the order is the simple articulation of the arm ossicles. The ambulacral plates are always opposite instead of being alternate, as in the Lysophiurae. In some of the most primitive genera the two ambulacral ossicles in an arm segment are separate, as in *Ophiurina*, or incompletely joined, as in *Ophiohelus*. In the Lapworthuridae they are firmly united, and in the recent genera *Ophiomyces* and its allies they are specialised into definite ambulacral ossicles, with a simple ball-and-socket articulation.

FAMILY 1. OPHIURINIDAE. Streptophiurae without ventral arm-plates and with separate ambulacral ossicles. Genera—*Ophiurina*, Stürtz, Devonian. *Tremataster*, Worthen & Miller.

FAMILY 2. LAPWORTHURIDAE. Streptophiurae without ventral arm-plates or buccal shields. Ambulacral ossicles fused, but their articulating surfaces are plain. Genera—*Lapworthura*, Greg., Silurian, W. of England ; *Furcaster*, Stürtz ; *Palastropecten*, Stürtz. The oral armament is typically Ophiuroid. The structure in the genus *Furcaster* is shown in Fig. XXXI. ; mouth-frames, small jaws, jaw plate, and teeth are all present.

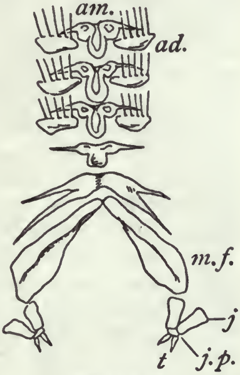


FIG. XXXI.

Furcaster palaeozoicus, Stürtz, showing skeletal elements of the arms and oral armament. *ad*, adambulacral ossicles bearing spines ; *am*, ambulacral ossicles ; *j*, jaw ; *j.p*, jaw plate ; *m.f*, mouth-frame ; *t*, teeth. (After Stürtz.)

FAMILY 3. EOLUIDIDAE. Streptophiurae with ambulacral ossicles united to form vertebral ossicles. Ventral arm-plates present, but there are neither buccal shields nor dorsal arm-plates. Genera—*Eoluidia*, Stürtz ; *Eospondylus*, Greg. ; *Miospondylus*, Greg. ; *Aganaster*, Miller & Gurley (syn. *Ophiopege*, Böhm) ; *Cholaster*, Worthen & Miller.

FAMILY 4. ONYCHASTERIDAE. Streptophiurae with well-developed vertebral ossicles, and very flexible, unbranched arms. There are no external arm-plates, the integument only containing granules. Genus—*Onychaster*, Carboniferous, Illinois, has previously been included among the Euryalid group, but its ambulacral ossicles (as shown by Meek and Worthen's later figures, *Geol. Surv. Illinois*, vol. v., 1873, pl. xvi. fig. 3d) are Streptospondyline.

FAMILY 5. EUCLADIIDAE. Streptophiurae with contorted branching arms. Five pairs of large plates round the centre of the side exposed in the fossil have been regarded either as jaws or as radial shields. Madreporite on same side as the plates. Arms have no external arm-plates but a granular integument. The type-species, *Eucladia Johnsoni*, was carefully figured and described by H. Woodward in 1869. Owing to its flexible, branched arms, and soft integument, it has generally been regarded as an ally of *Euryale*, but some authors have urged its removal to the Asteroidea, ascribing a dorsal position to the madreporite. It is no doubt in external appearance more like the Cladophiurae than the Streptophiurae, but the external resemblance to *Euryale* is probably due to homoplastic modifications.

FAMILY 6. THE LIVING STREPTOPHIURAE. No attempt has yet been made to arrange the living Streptophiurae into families, and this cannot be done with advantage without further knowledge about several points. Some of the most remarkable genera are known only by single specimens, which are very small and probably immature. *Ophiohelus* and *Ophiotholia* present a certain resemblance to the *Lysophiurae* in the structure of the ambulacral ossicles. *Ophiogeron*, with its long, rod-shaped, ambulacral ossicles lying in opposite pairs, is much like *Ophiurina*, but the evidence available at present is insufficient to justify its inclusion in the Ophiurinidae. Hence it is advisable at present to leave the living Streptophiurae arranged according to Bell's scheme (3). When the classification is attempted, probably *Ophioteresis* will form one family, and *Ophiosciasma* another; *Hemieuryale*, *Sigsbeia*, *Ophiochondrus*, and *Ophiomyces* may constitute a third.

A. No under arm-plates—*Ophioteresis*, Bell.
B. Under arm-plates imperfect—*Ophiosciasma*, Lym.
C. Under arm-plates moderate or well developed.
α. No upper arm-plates—I. No radial shield—*Neoplax; Ophiohelus*, Lym.; *Ophiotholia*, Lym. (?). II. Radial shields present—*Ophioscolex*, Müll. & Trosch.; *Ophiambix*, Lym.; *Ophiogeron*, Lym..; *Ophiobyrsa*, Lym.; *Ophiomyxa* (pars), Müll. & Trosch.
β. Upper arm-plates minute or formed of scattered plates—*Ophiomyxa* (pars), Müll. & Trosch.; *Ophiomyces*, Lym.; *Ophiochondrus*, Lym.; *Hemieuryale*, Martens; *Sigsbeia*, Lym.

ORDER 3. **Cladophiurae**, Bell (1892).

Ophiuroidea in which the vertebral ossicles articulate with one another by means of hour-glass-shaped surfaces (Fig. XXXIII.), and are covered by granular deposits in the thick integument. The arms may be simpie or branched repeatedly.

FAMILY 1. ASTRONYCIDAE. Cladophiurae with simple unbranched arms. GROUP 1. With large disc—*Astrotoma*, Lym.; *Astromyx*, Müll. & Trosch.; *Astrochele*, Verr. GROUP 2. Disc of medium size—*Astrogomphus*, Lym.; *Astroporpa*, Oersted & Lütken. GROUP 3. Disc small—*Ophiocreas*, Lym.; *Astroschema*, Oerst. & Lütk.; *Astroceras*, Lym. FAMILY 2. TRICHASTERIDAE. Cladophiurae with arms branching a few times near their free ends. Genera, recent—*Trichaster*, L. Ag.; *Astroclon*, Lym.; *Astrocnida*, Lym. Fossil—*Astrocnida*, Lym. FAMILY 3. GORGONOCEPHALIDAE. Cladophiurae with arms branching much and from their base. *Euryale*, Lam.; *Gorgonocephalus*, Lym.; *Astrophyton*, Ag. (Fig. XXXII.) *Ophiocrene*, Bell.

ORDER 4. **Zygophiurae**, Bell (1892).

Ophiuroidea in which the movement of the ossicles on one another is limited by the development of lateral processes and pits. Superior, inferior, and lateral spine-bearing arm-plates are always present. The arms are simple and cannot coil round straight rods.

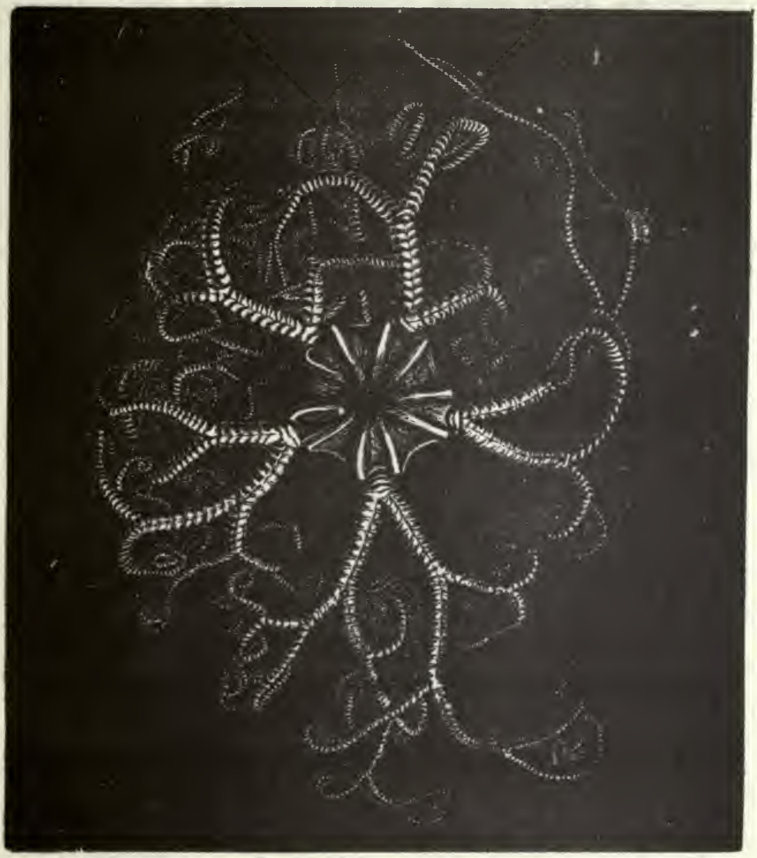


FIG. XXXII.

Astrophyton Lincki. Abactinal surface. (From Wyv. Thomson.)

FAMILY 1. OPHIODERMATIDAE. Zygophiurae with oral papillae numerous, and none infra-dental. Arm incisures on the disc. Dental papillae absent. Genera—*Ophioderma*, Müll. & Trosch. ; *Ophiopeza*, Peters ; *Ophiarachna*, Müll. & Trosch.; *Ophiocoeta*, Lütk.; *Ophioconis*, Lütk.; *Ophioplax*, Lym. ; *Ophiogona*, Stud. ; (?) *Ophiopyrgus*, Lym. ; *Ophiopyren*, Lym.

Family 2. Ophiolepididae. Zygophiurae with oral papillae from three to six, of which the last may be infra-dental. Arm incisures on the disc. Dental papillae absent. Genera—*Ophiolepis*, Müll. & Trosch.; *Ophiocten*, Lütk.; *Ophiura*, L. Ag.; *Ophioglypha*, Lym.; *Ophioceramis*, Lym.; (?) *Ophiochiton*, Lym.; *Ophiopaepale*, Lym.; *Ophiozona*, Lym.; *Ophioplinthus*, Dan.; *Ophiernus*, Lym.; *Amphiglypha*, Pohl.; *Geocoma*, d'Orb.

Family 3. Amphiuridae. Zygophiurae with oral papillae from one to five, of which the last is generally infra-dental. Arms inserted on ventral side of disc. Dental papillae absent. Genera—*Amphiura*, Forbes; *Ophiocnida*, Lym.; *Ophiomusium*, Lym.; *Ophiopeltis*, Daniels. & Kor.; *Ophiocentrus*, Ljung.; *Amphilepis*, Ljung.; *Ophiolepis*, Lym.; *Ophiomartus*, Lym.; *Ophiophyllum*, Lym.; *Ophiotrochus*, Lym.; *Hemipholis*, Lym. (Fig. XXXIII.); *Ophiactis*, Lütk.; *Ophiopus*, Ljung.; *Ophiopholis*, Lütk. (Fig. XIII.); *Ophiacantha*, Müll. & Trosch.; *Ophiotrema*, Koehl.; *Pectinura*, Heller (*non* Forbes); *Ophioplocus*, Lym.; *Ophionereis*, Lütk.; *Amphipholis*, Ljung.; *Ophiophragonus*, Lym.; *Ophiostigma*, Lütk.; *Ophioblenna*, Lütk.; *Ophiocymbium*, Lym.; *Ophiochytra*, Lym.; *Ophiolebes*, Lym.; *Ophiomitra*, Lym.; *Ophiocamax*, Lym.; *Ophiothamnus*, Lym.; *Acroura*, Ag.; *Aspidura*, Ag.; *Hemiglypha*, Pohl.; *Polypholis*, Dunc.

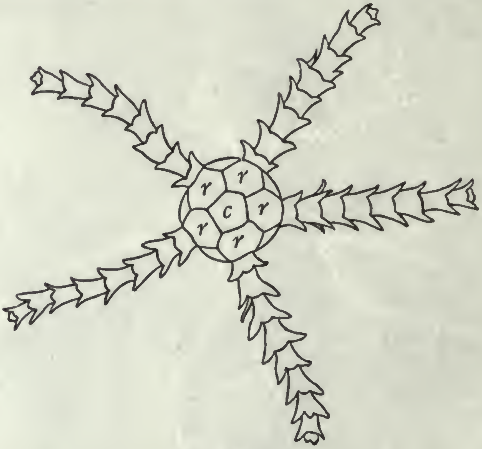


Fig. XXXIII.

Abactinal view of *Hemipholis cordifera*, Lym. *c*, central plate; *r*, plates of radial circlet.

Family 4. Ophiocomidae. Zygophiurae with both oral and dental papillae. Genera—*Ophiocoma*, L. Ag.; *Ophiomastix*, Müll. & Trosch.; *Ophiarthrum*, Pet.; *Ophiopsila*, Forbes; *Ophiopteris*, E. A. Smith.

Family 5. Ophiothricidae. Zygophiurae with dental papillae, but no oral papillae. Genera—*Ophiothrix*, Müll. & Trosch.; *Ophiocnemis*, Müll. & Trosch.; *Ophiogymna*, Ljung.; *Ophionema*, Lütk.; *Ophionephthys*, Lütk.; *Ophiomaza*, Lym.; *Ophiothela*, Verr.; *Ophiopsammium*, Lym.; *Ophiopteron*, Ludw.; (?) *Ophiurella*, Ag.

THE LITERATURE OF STELLEROIDEA.

1. *Agassiz, A.* 1877. (North American Starfishes.) Mem. Mus. Comp. Zool.-Harvard, vol. v. No. 1, v. and 136 pp., xx. pls.
2. *Apostolidès, N. C.* 1882. (Anatomie et développement des Ophiures.) Arch. Zool. Expér., sér. 1, tom. x. pp. 121-224, pls. vii.-xii.
3. *Bell, F. J.* 1892. (A Contribution to the Classification of Ophiuroids, &c.) Proc. Zool. Soc. for 1892, pp. 175-183, pls. xi., xii.
4. —— 1892. Catalogue of the British Echinoderms in the British Museum (Natural History), 8vo, xvii. and 202 pp., xvi. pls. London.
5. *Billings, E.* 1858. (On the Asteriadae of the Lower Silurian Rocks of Canada.) Canad. Org. Rem., dec. iii. pp. 75-85, pls. viii.-x.
6. *Bury, H.* 1889. (Studies in the Embryology of the Echinoderms.) Quart. Journ. Micro. Sci., N.S. vol. xxix. pp. 409-449, pls. xxxvii.-xxxix.
7. *Carpenter, P. H.* 1882. (Notes on Echinoderm Morphology. No. V. On the Homologies of the Apical System, with some Remarks upon the Blood-Vessels.) Quart. Journ. Micr. Sci., N.S. vol. xxii. pp. 371-386.
8. *Cuénot, L.* 1887. (Contribution à l'étude anatomique des Astérides.) Arch. Zool. Expér., sér. 2, vol. v. bis. suppl., 144 pp., ix. pls.
9. —— 1888. (Études anatomiques et morphologiques sur es Ophiures.) Arch. Zool. Expér., sér. 2, vol. vi. pp. 33-82, pls. iii.-v.
10. *Danielssen, D. C., and Koren, J.* 1884. The Norwegian North Atlantic Expedition, 1876-78. Zoology, Asteroidea, 119 pp., xv. pls.
11. *Forbes, E.* 1840-41. A History of British Starfishes, and Other Animals of the Class Echinodermata, 8vo, xx. and 270 pp. London.
12. —— 1849-50-56. Figures and Descriptions of British Organic Remains. Decades i., iii., v.
13. *Gaudry, A.* 1852. (Mémoire sur les pièces solides des Stellérides.) Ann. Sci. Nat. Zool., sér. 3, vol. xvi. pp. 339-379.
14. *Gray, J. E.* 1866. Synopsis of the Species of Starfish in the British Museum, 8vo. London.
15. *Gregory, J. W.* (The Classification of the Palaeozoic Echinoderms of the Group Ophiuroidea.) Proc. Zool. Soc. for 1896, pp. 1028-1044.
16. *Hall, James.* 1867. (Note upon the Genus Palæaster and Other Fossil Starfishes.) Reg. Rep. State Cab. Nat. Hist. N.Y., No. xx. pp. 282-303, pl. ix.
17. *Hamann, O.* 1885-89. Beiträge zur Histologie der Echinodermen. Heft 2. Die Asteriden, &c., 8vo, Jena. Heft 4. (Anat. und Histol. der Ophiuren und Crinoiden), Jena. Zeitschr., vol. xxiii. pp. 233-388, pls. xii.-xxiii.
18. *Heller, Camill.* 1858. (Ueber neue fossile Stelleriden.) Sitz.-ber. math.-nat. Cl. Akad. Wiss. Wien, vol. xxviii. pp. 155-170, pls. i.-v.
19. *Hoffmann, C. K.* 1874. (Zur Anatomie der Asteriden.) Niederl. Arch. Zool., vol. ii. pp. 1-32, pl. i.-ii.
20. *Koehler, R.* 1887. (Recherches sur l'appareil circulatoire des Ophiures.) Ann. Sci. Nat. Zool., ser. 7, vol. ii. pp. 101-158, pls. vii.-ix.
21. *Lamarck, J. B. P. A. de M.* 1816. Histoire naturelle des Animaux sans Vertèbres, vol. ii., 8vo. Paris.
22. *Lange, W.* 1876. (Beiträge zur Anatomie und Histiologie der Asterien und Ophiuren.) Morph. Jahrb., vol. ii. pp. 241-286, pls. xv.-xvii.

23. *Linck, J. H.* 1733. De Stellis, Marinis etc. Fol., xxiv. and 107 pp., xlii. pls. Lipsiae.
24. *Ljungman, A.* 1866. (Ophiuroidea viventia huc usque cognita.) Öfvers. Svensk. Vet. Akad. Förhandl., 1866, No. 9, pp. 303-336.
25. *Ludwig, H.* 1877-82. Morphologische Studien an Echinodermen, 8vo. Leipzig. Reprinted from Zeitschr. Wiss. Zool. vol. xxx. pp. 99-162, pls. v.-viii.; vol. xxxi. pp. 59-67, pl. v.; pp. 216-234, pl. xv.; pp. 346-400, pls. xxiv.-xxviii.; vol. xxxii. pp. 672-688; vol. xxxiv. pp. 333-366 pls. xiv.-xvi.; vol. xxxvi. pp. 181-200, pls. x., xi.; vol. xxxvii. pp. 1-98 pls. i.-viii.
26. —— 1888. (*Ophiopteron elegans*, eine neue, wahrscheinlich schwimmende Ophiuridenform.) Zeit. Wiss. Zool. vol. xlvii. pp. 459-464, pl. xxxv.
27. *Lütken, C. F.* 1858-59. Additamenta ad historiam Ophiuridarum, Videnskab. Selsk. Skrifter (5), Naturvid. og Math. Afd. vol. v. pp. 1-74, pls. i., ii.; pp. 177-272, pls. i.-v.
28. *Lyman, Th.* 1865. (Ophiuridae and Astrophytidae.) Ill. Cat. Mus. Comp. Zool. Harvard, No. 1, viii. 200 pp., ii. pls.
29. —— 1871. (Supplement to the Ophiuridae and Astrophytidae.) Ill. Cat. Mus. Comp. Zool. Harvard, No. 6, 18 pp., ii. pls.
30. —— 1874. (Ophiuridae and Astrophytae, new and old.) Bull. Mus. Comp. Zool. Harvard, vol. iii. No. 10, pp. 221-272, vii. pls.
31. —— (Report on the Ophiuroidea dredged by H.M.S. *Challenger* during the years 1873-76.) Rep. Chall. Zool. vol. v. 1882, 4°, pp. 387, 48 pls.
32. *MacBride, E. W.* 1892. (The development of the genital organs, ovoid gland, axial and aboral sinuses in *Amphiura squamata*, together with some remarks on Ludwig's haemal system in this Ophiurid.) Quart. Journ. Micr. Sci., N.S., vol. xxxiv. pp. 129-153, pls. xvi.-xviii.
33. —— 1896. (The Development of *Asterina gibbosa*.) Quart. Journ. Micr. Sci., N.S., vol. xxxviii. pp. 339-411, pls. xviii.-xxix.
34. *Müller, Joh.* 1854. (Über den Bau der Echinodermen.) Phys. Abh. Akad. Wiss. Berlin, Jahrg. 1853, pp. 123-219, pls. i.-ix.
35. —— *& Troschel, F. H.* 1840. (Über die Gattungen der Asterien, und der Ophiuren.) Arch. f. Naturg., Jahrg. 6, Bd. i. pp. 138-328, 367-368.
36. —— 1842. System der Asteriden. 4to, pp. xx. and 135, xii. pls. Braunschweig.
37. *Perrier, J. O. E.* 1875-76. (Revision de la collection de Stellerides.) Arch. Zool. Exper., vols. iv. and v.
38. —— 1894. Expéditions Scientifiques du *Travailleur* et du *Talisman* pendant les années 1880, 1881, 1882, 1883. Échinodermes, pt. 1. 4°, pp. iv. and 431, xxvi. pls.
39. —— 1891. Mission Scientifique du *Cap Horn*, 1882-83, tom. vi. Zoologie Echinodermes, I., Stellérides. 4to, Paris, 198 pp., xiii. pls.
40. —— 1891. (Stellérides nouveaux provenant des Campagnes du yacht *l'Hirondelle*.) Mém. Soc. Zool. France, vol. iv. pp. 258-271.
41. *Prouho, H.* 1890. (Du sens de l'odorat chez les Étoiles de Mer.) Compt. Rend. Acad. Paris, vol. cx. pp. 1343-46.
42. *Salter, J. W.* 1857. (On some new Palaeozoic Starfishes.) Ann. Mag. Nat. Hist. ser. 2, vol. xx. pp. 321-334, pl. ix.
43. *Sars, G. O.* 1875. Researches on the Structure and Affinities of the Genus *Brisinga*, etc. 4to, 111 pp., vii. pls. Christiania.

44. *Schulze, C. F.* 1760. Betrachtung der versteinerten Seesterne und ihrer Theile. 4to, vi. and 58 pp., ii. pls. Warschau und Dresden.
45. *Simonowitsch, Spiridon.* 1871. (Ueber einige Asteroiden der rheinischen Grauwacke.) Sitzber. math.-phys. Cl. Akad. Wiss. Wien, vol. lxiv., Abt. 1, pp. 77-122, iv. pls.
46. *Simroth, H.* 1876-77. (Anatomie und Schizogonie der *Ophiactis virens.*) Zeitschr. Wiss. Zool., vol. xxvii. pp. 417-485, pls. xxxi.-xxxv.; vol. xxviii. pp. 419-526, pls. xxii.-xxv.
47. *Sladen, W. P.* 1879. (On the Structure of *Astrophiura,* a new and Aberrant Genus of Echinoderms.) Ann. Mag. Nat. Hist., ser. 5, vol. iv. pp. 401-415, pl. xx.
48. —— 1889. (Report on the Asteroidea collected by H.M.S. *Challenger* during the years 1873-76.) Rep. Chall. Zool., vol. xxx. 893 pp., cxvii. pls.
49. *Stürtz, B.* 1886. (Beitrag zur Kenntniss palaeozoischer Seesterne.) Palaeontographica, vol. xxxii. pp. 75-98, pls. viii.-xiv.
50. —— 1890. (Neuer Beitrag zur Kenntniss palaeozoischer Seesterne.) Palaeontographica, vol. xxxvi. pp. 203-247, pls. xxvi.-xxxi.
51. —— 1893. (Ueber versteinerte und lebende Seesterne.) Verh. Naturh. Ver. Preuss. Rheinl., vol. l. pp. 1-92, pl. i.
52. *Viguier, C.* 1879. (Anatomie comparée du Squelette des Stellérides.) Arch. Zool. Expér., vol. vii. 1878, pp. 33-250, pls. v.-xvi.
53. *Woodward, H.* 1869. (On *Eucladia,* a new genus of Ophiuridae.) Geol. Mag., N.S., vol. vi. pp. 241-245, pl. viii.
54. *Wright, Th.* British Fossil Echinodermata of the Oolitic Formations. Vol. ii. The Asteroidea and Ophiuroidea. Palaeontogr. Soc. 1863-80.

CHAPTER XV.

THE ECHINOIDEA.[1]

CLASS III. ECHINOIDEA.

SUB-CLASS 1. REGULARIA ENDOBRANCHIATA.
  Order 1. **Bothriocidaroida.**
  ,, 2. **Cystocidaroida.**
  ,, 3. **Cidaroida.**
  ,, 4. **Melonitoida.**
  ,, 5. **Plesiocidaroida.**

SUB-CLASS 2. REGULARIA ECTOBRANCHIATA.
  Order 1. **Diademoida.**
    Sub-Order 1. **Calycina.**
    ,, 2. **Arbacina.**
    ,, 3. **Diademina.**
    ,, 4. **Echinina.**

SUB-CLASS 3. IRREGULARIA.
  Order 1. **Gnathostomata.**
    Sub-Order 1. **Holectypina.**
    ,, 2. **Clypeastrina.**
  Order 2. **Atelostomata.**
    Sub-Order 1. **Asternata.**
    ,, 2. **Sternata.**

KNOWLEDGE of the Echinoidea or Sea Urchins is more complete than that of any other of the classes of Echinoderma. The class is widely distributed at the present day, members of it living in seas of all parts of the world and at all depths. It is of great antiquity, and fossil Echinoids occur abundantly in rocks of all periods since the Devonian, while a few are known from that system and from the Silurian. Moreover, as the classification of the Echinoids depends either upon the skeleton, or upon structures, the characters of which can be inferred from those of the skeleton, the systematic position of a fossil can generally be determined with as much accuracy as that of a recent specimen.

---

[1] By J. W. Gregory, D.Sc. MS. closed at end of 1896.

The very varied habits of the Echinoids further increase the value of this class. Some sea-urchins burrow into sand, and others bore into rocks. Some seek the shelter of rock-pools or the quiet of a muddy sea-floor below the limit of tidal action. Others cling to rocks between tide-lines, choosing the positions that are most exposed to the buffeting of a tropical surf; others again crawl over, or lie half-buried in, the ooze of abyssal oceanic depths. Some feed on algae; others swallow mud and live on the organic matter it contains. Of some the young develop directly, of others indirectly, the latter undergoing a metamorphosis during development. The modifications in structure by which Echinoids are able to adapt themselves to these different habits are so well marked, that the conditions under which fossil sea-urchins lived can generally be determined. Hence the group is of great value to the geologist. Such rich series of Echinoid faunas are known, that the life-history of the class can be written with greater completeness than that of any other group of Echinoderms, and as completely as that of any class in the animal kingdom.

Little, however, is certainly known as to the relations of the Echinoidea to other Echinoderms. The group is so compact and well marked, that the distinction between it and the other classes was known to Aristotle, and has never been in doubt. Moreover, the class has been as well defined as it now is since Silurian times. The recognition of the sea-urchins as a distinct group of Echinoderms is, therefore, as old as zoology. A sketch of the history of work upon the Echinoids need only consider the determination of the main points in their anatomy, life-history, and classification.

The earliest account of the natural history of the sea-urchins is in Aristotle's *History of Animals*, wherein the common edible species of the Mediterranean (*Echinus esculentus*) is described with considerable accuracy. Aristotle called this animal *Echinus* (Eχῖνος), the Greek for hedgehog, a term subsequently given to the best known genus, and used as the root of the name for the class. In the same book three other types of sea-urchins are mentioned, viz. *Brissus*, *Spatangus*, and *Echinometra;* and these names are still used in Echinoid nomenclature. Aristotle's account shows that he had studied both the habits and anatomy of the animals; thus he knew that *Echinus* could walk upon the tip of its spines, had five teeth, five unpaired ovaries, a pharynx, and stomach. In mediaeval times Echinoids were described by Rondelet (1554) and Aldrovandus (1606 and 1648); but it was not till the beginning of the eighteenth century that any observations of scientific value were published. The first important post-classical contributions to the subject were the works of Breynius (1732) and Klein (1734). The former in his *De Echinis et Echinitis*, and the latter in his *Naturalis Dispositio Echinodermatum*, figured and described many genera and species of Echinoids; but, as their names were not binominal, they are not accepted. Gualtieri in 1742, and Seba in 1758, used the names and methods of their predecessors, and described additional species. In the latter year Linnaeus adopted the binominal system of nomenclature in the tenth edition of his *Systema Naturae*, but in other respects his treatment of the Echinoids was retrograde. He accepted sixteen species; but although among these there were such different types as *Echinus esculentus*, *Cidaris*, *Echinometra*, *Colobocentrotus*, *Arachnoides*, *Clypeaster*, etc., he included them all within a single genus. He thus threw back the study of Echinoids for twenty years. It was not till 1778 that Leske (48) reintroduced the sound system of work adopted by Breynius and Klein, which had been discarded by Linnaeus. Leske's edition of Klein, with his own "Additamenta," therefore forms the real starting-point of systematic Echinology. No important advance from this was made until the publication of Lamarck's *Histoire Naturelle des Animaux sans Vertèbres* in 1816.

From this date progress was rapid;[1] the principal contributions being made by Gray (1825), de Blainville (1830), Desmoulins (1837), L. Agassiz (1836, 1840, 1841, 1842), and Desor (1842). In 1846 and 1847 the last two authors published a complete synopsis of knowledge up to that date in their *Catalogue Raisonné des Echinides*. Since then the literature of the Echinoidea has been voluminous. The existing species have been described by Lütken, Düben and Koren, Lovén, Leuckart, Peters, Grube, Döderlein, Thomson, Bell, and especially by A. Agassiz. Our knowledge of Palaeozoic Echinoids is mainly due to M'Coy, C. F. Römer, J. Müller, Desor, Meek, Worthen, Hall, Neumayr, Duncan, Keeping, and Jackson; of the Mesozoic faunas to d'Orbigny, Cotteau, Wright, de Loriol le Fort, Clark, Schultze, Lambert, Gras, Forbes, S. P. Woodward, etc.; of the Cainozoic to Dames, Laube, Cotteau, de Loriol, Forbes, Bittner, Gauthier, Peron, Pomel, Duncan, Sladen, Hutton, Sismonda, Michelin, Grateloup.

Dujardin and Hupé (21) in 1862 attempted a synopsis of the whole of the Echinoidea. Desor's *Synopsis des Echinides Fossiles* (1854-58) is the last reliable summary of the fossil species, as is Agassiz's *Revision of the Echini* of the recent. Revisions of the genera were arranged by Pomel in 1883 and Duncan in 1890 (24).

The morphology of the Echinoidea was first seriously studied by L. Agassiz and Valentin, whose account in 1842 (5) of the skeleton and visceral anatomy was based mainly on *Strongylocentrotus lividus*, Lam. sp. The circulation had been previously described by Tiedemann (1815) and Delle Chiaje (1825), and the nerves by Krohn

---

[1] Reference to part of the literature is given on pp. 328-332; a bibliography up to 1872 is given by A. Agassiz (1), pp. 1-9. Some of the general works are included in the lists for Stelleroidea (p. 279) and for Echinoderma generally (p. 35).

(1841). The next important advance was made by the memoirs of Joh. Müller (1850-57) who gave a full account of *Cidaris*. Among later general contributions to anatomy may be mentioned those of Teuscher (1876), Koehler (1883), Prouho (1887), Frédéricq (1876), Perrier (1869 and 1875), Hamann (1889), and the last part of A. Agassiz's *Revision*. Special types have been described in separate memoirs, such as *Cidaris* and its internal branchiae, by Stewart (1880); *Spatangus*, by Hoffmann (1871); *Asthenosoma*, by P. and F. Sarasin (1888); *Phormosoma*, by Bell (1889); *Dorocidaris*, by Prouho (1888); *Pourtalesia*, by Lovén (1883).

Knowledge of the anatomy of the skeleton is due to many students, but especially to the masterly series of memoirs by Lovén. The structure of the spines has been described and their taxonomic value shown by Mackintosh (63) and A. Agassiz (1, 2); the fascioles were first used in classification by Lütken. The pedicellariae were first described by O. F. Müller, who regarded them as parasites, a view disproved by Delle Chiaje; L. Agassiz considered them to be young *Echini*, which was shown to be erroneous by Valentin's detailed figures. An attempt to use pedicellariae as a basis for classification was made by Perrier (1869-70); their function has been the subject of a long controversy.

The study of the embryology of Echinoidea was begun by Derbès in 1847, and by Müller in a series of memoirs (1848-55); it was continued by Krohn (1849-57), A. Agassiz (1864), Metschnikoff (1868-69), Bury (1889 and 1895), Théel (1892), MacBride (1896), and others.

The term Echinoidea, now used as the name of the class, was applied by Aristotle to animals that resembled *Echinus*, which has always been regarded as the most representative genus. Though in some ways rather complex, it may be conveniently studied as a **Typical Sea-Urchin**, since specimens can be easily obtained.

The Skeleton. If we examine a specimen of the common British species *Echinus esculentus*, we first notice that it is covered all over by short, bluntly pointed spines, which are coloured violet at the tips. If we pull off the longest spines, we find between them a number of smaller "secondary" spines (compare Fig. XXXIII.). After removal of all the spines, the general character of the main shell can be seen. It is composed of closely fitting plates, which together form the rigid "test" or shell. The shape is rounded in transverse section; the surface on which the mouth opens is flattened, while the upper half of the test may be either well rounded or sub-conical.

On the centre of the lower flattened surface there is a large flexible membranous area covered with loose plates which bear short spines. This is the "peristome"; the mouth opens in the centre of this space; its exact position can be determined by the presence of five sharp teeth, which, if not extruded so as to be seen, can at once be felt. At the other end of the axis of the body there is a smaller membranous area, the "periproct," in the centre of which is the anus. The periproct is surrounded by a circle of five plates (Fig. I.), one of which is larger than the rest; this large plate bears a small perforated prominence, called the "madreporiform tubercle" or "madreporite" (*m*). Through the pores in this plate water passes to the series of canals known as the water-vascular system. Each of the other four plates of this apical circle is perforated by one of the pores through which the genital products escape to the exterior. These five plates are therefore known as the "genitals" (*g*). Alternating with them are five smaller plates (*o*), each perforated by a pore, through which passes a process ending in a sensory eye-spot. These plates are therefore called the "oculars." The whole ten plates form a group known as the "apical system." Between the apical system and the peristome is the main test. Ten lines of suckers may be seen in a fresh specimen, radiating from the five ocular plates; two lines start from each ocular, and pass in a straight series round the test to the edge of the peristome. As the two series of suckers are arranged like the rows of trees in an avenue, the area bounded by them has been called an *ambulacrum*.[1] As there is one ambulacrum to each ocular, there are five in the complete test, separated by five broader *interambulacra*.

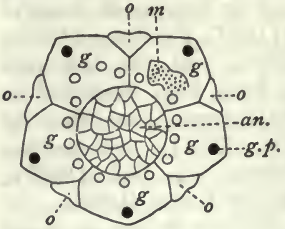
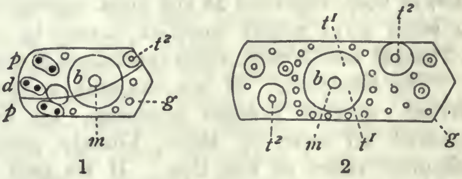


Fig. I.

Echinus esculentus, Linn., apical system and periproct. *m*, madreporite; *g*, genital plates; *g.p*, genital pore; *o*, ocular plates; *an*, anal plates covering the periproct, in the centre of which opens the anus.

Fig. II.

Ambulacral (1) and interambulacral (2) plates of *Echinus esculentus*. t^1, t^2 are the primary and secondary tubercles; *g*, miliary granules; *p*, primary ambulacral plate; *d*, epipodium with a pore pair; *b*, boss; *m*, mamelon.



Each ambulacrum and interambulacrum consists of a double row of plates in vertical series running from the apical system to the peristome. Each interambulacral plate (Fig. II. 2) is irregularly pentagonal in form; the angles are sharp and regular, but the plate is elongated in a horizontal direction. Each plate bears a number of "tubercles," of which there are three sizes—primary

---

[1] From *ambulacrum*, an avenue or a walk between trees.

(t^1), secondary (t^2), and miliary (g). The primary tubercles are the largest, and bear the primary spines; each tubercle consists of a rounded base or "boss" (b), on the centre of which is a small pimple or "mamelon" (m). Around the base of each primary tubercle is a smooth, level surface called the "scrobicule," which is generally surrounded by a circle of granules called the "scrobicular circle." Scattered irregularly over the plates are the smaller secondary tubercles which bear the secondary spines, and between these are large numbers of smaller elevations known as "miliary granules" (g).

The function of these tubercles and granules is the support of the appendages known as "spines" and "pedicellariae." The Spines, like the tubercles, are of three sizes — primary, secondary, and tertiary—the structure of each of which is fundamentally the same. Each consists of a long shaft, marked by longitudinal flutings; the base of the spine is hollowed into a cup or condyle, which fits over the mamelon of the tubercle. Around the condyle is the collar of the spine which projects above the level of the shaft, and serves for the attachment of the muscles which fix it to the test. A transverse section of the spine (Fig. III.) shows that it is made up of a number of solid wedges, radiating from a central axis, and separated by bands of porous tissue.[1] The smallest spines consist only of tiny needles of porous tissue, and agree in structure with the spines of the second type of appendage.

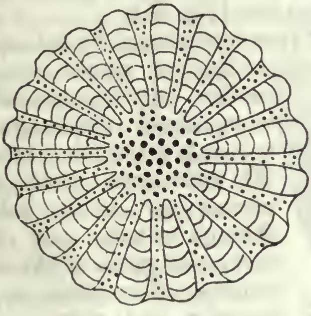


FIG. III.

Appendages of *Echinus*. Transverse section of spine (magnified).

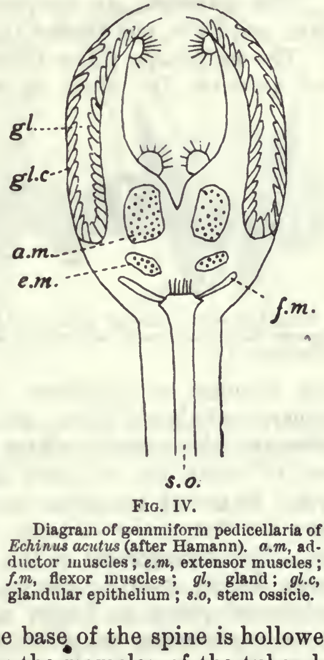


FIG. IV.

Diagram of gemmiform pedicellaria of *Echinus acutus* (after Hamann). *a.m*, adductor muscles; *e.m*, extensor muscles; *f.m*, flexor muscles; *gl*, gland; *gl.c*, glandular epithelium; *s.o*, stem ossicle.

The *pedicellariae* (Fig. IV.) consist of two or three beak-like valves attached to the end of a flexible stem. The valves open and shut like a bird's beak, or like the avicularia of Bryozoa. They have been seen to seize particles of the excreta of the urchin and pass them on from one pedicellaria to another, until they fall over the margin of the test. Their main function, however, appears to be defensive. When a starfish attacks a sea-urchin, the latter bends down its spines and thus exposes its pedicellariae; these seize hold of the tube-feet of the starfish, which their bites appear to hurt. The pedicellariae, however, are always torn away, as they cannot relax their hold; and thus, if an urchin is attacked by a series of starfish, it is in time rendered defenceless (Prouho, 70).

---

[1] The spine is therefore, according to the terminology of Mackintosh (63), polycyclic and acanthosphenote.

The *sphaeridia* are also modified spines; they are globular in form, and lie in pits around the peristome (Fig. V.).

The ambulacral plates (Fig. II. 1) are ornamented by tubercles and granules like those of the interambulacral plates, though smaller; but the plates differ in structure. The interambulacrals are solid, whereas the ambulacral plates are pierced by small holes, through which pass the suckers or podia of the ambulacra. The pores occur in pairs, and each pair is surrounded by a raised ring forming an *epipodium*. There is one epipodium to each primary ambulacral plate; but, except at the summit of the ambulacrum, the primary plates are united into compound plates, each of which has as many epipodia as there are primary plates in it. In one of the plates in the middle of the ambulacral series there are three pairs of pores, which occur in a curved series or arc. This arrangement of the pairs is due to the crowding of the plates during growth; owing to the same cause, the elementary ambulacral plates no longer always extend right across the half of the ambulacrum to which they belong, but are cut off from the median suture by the union of adjoining plates behind them. Plates thus cut off from the central suture line are known as "demi-plates." In an ordinary *Echinus esculentus* each compound ambulacral plate (Fig. XII. 4) consists of one central demi-plate (*d*) between two primary plates (*p*).

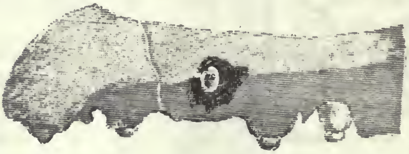


FIG. V.

Transverse section through peristomial plates of *Clypeaster* showing a globular sphaeridium in its pit. (After Lovén.)

The principal remaining elements in the skeleton are those of the five jaws, and of the internal processes, to which the muscles that work the jaws are attached. The Dental Apparatus (Fig. VI.) is a conical structure which is placed apex downwards over the mouth. The axis is hollow and contains the pharynx or commencement of the oesophagus. The dental apparatus consists of twenty pieces. The largest of these are the five pyramids (Fig. VI. *p*); they are shaped like the sectors of a cone, being pointed at one end, having two flat sides, and with a curved outer margin. The flat sides are marked by transverse ridges, which serve for the attachment of the muscles that bind the pyramids to one another. The pyramids are hollow, and in each of them lies a long, curved, keeled tooth, the hard point of which projects through a hole at the pointed lower end of the pyramid. Above the suture between a pair of pyramids rests a short, thick bar known as the brace; above the brace (*b*) is a curved bifid process or "compass" (*cp*).

Round the inside of the peristome is a hard raised rim (Fig. VII. *p.r*) which rises into an arch over each of the ambulacra. This is the "perignathic girdle," and to it are attached the muscles which work the masticatory apparatus; one set of muscles attached to the pyramid pulls the jaws apart; other sets, attached to the braces and compasses, pull them downward and drive the teeth together.

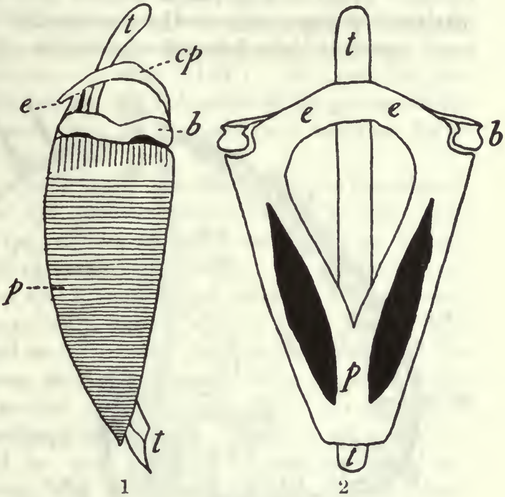


FIG. VI.

Dental apparatus of *Echinus esculentus*, L. A pyramid seen from the side (1), and from behind (2); *p*, pyramid; and *e*, its epiphysis; *t*, tooth; *b*, brace; *cp*, compass.

The remaining skeletal structures are small and unimportant, and consist only of scattered calcareous plates and spicules which are distributed through the tissues. The principal of these are the "rosettes" or "pellions" (rings of plates which support the suckers), and spicules in the stems of the podia.

The internal anatomy of the *Echinus* may be most conveniently studied by the removal of the upper half of the test. The five ovaries will then be seen lying in the upper parts of the interradia, and the great coiled intestine occupying most of the interior. The main features in the internal anatomy are shown in Fig. VII.

The Alimentary Canal begins with a mouth (*mt*) situated at the centre of the peristomial membrane (*pst*); from the mouth the muscular pharynx (*ph*) passes upwards through the central tube of the masticatory apparatus. The oesophagus (*oe*) runs horizontally from the upper end of the pharynx to the lobed stomach (*s*), which is twisted in a spiral twice round the body cavity; it contracts above to the rectum (*r*), which opens to the exterior by an anus (*a*), situated in the centre of the apical system.

The Water-vascular System. Above the top of the dental apparatus a vessel may be seen running round the oesophagus. This is the circumoesophageal ring of the water-vascular system (*c.œ.v*). From it five radial vessels pass downwards outside the masticatory apparatus to the peristomial membrane; there they bend upwards, pass beneath the arches of the perignathic girdle (*p.a*), and one runs up the inside of each ambulacrum. Branches from the radial vessels are given off alternately to right and left; one of these branches passes to each pore-pair, below which it opens to a pair of pocket-shaped vesicles or ampullae (*ap*). From each ampulla a small tube passes through both pores; the two tubes unite on the exterior to form the shaft of the tube-foot or podion (*pd*).

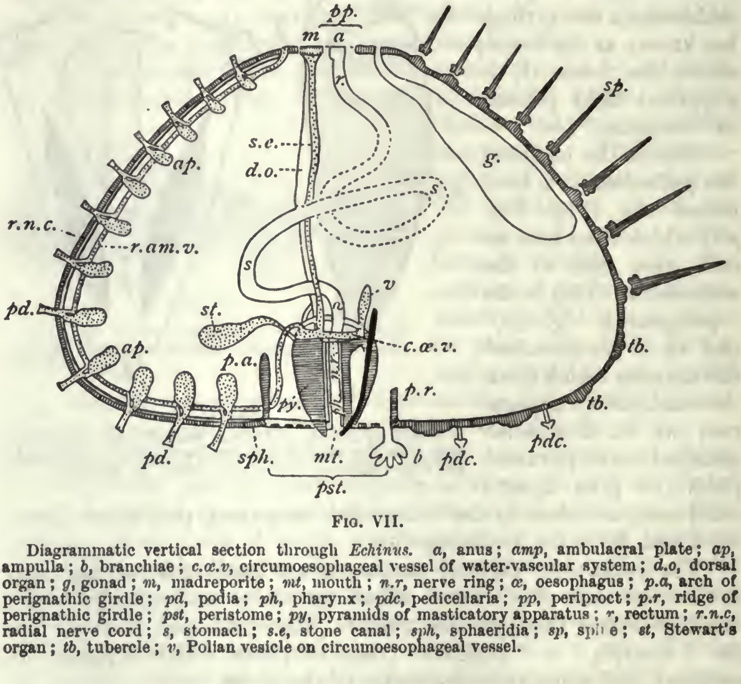


FIG. VII.

Diagrammatic vertical section through *Echinus*. *a*, anus; *amp*, ambulacral plate; *ap*, ampulla; *b*, branchiae; *c.œ.v*, circumoesophageal vessel of water-vascular system; *d.o*, dorsal organ; *g*, gonad; *m*, madreporite; *mt*, mouth; *n.r*, nerve ring; *œ*, oesophagus; *p.a*, arch of perignathic girdle; *pd*, podia; *ph*, pharynx; *pdc*, pedicellaria; *pp*, periproct; *p.r*, ridge of perignathic girdle; *pst*, peristome; *py*, pyramids of masticatory apparatus; *r*, rectum; *r.n.c*, radial nerve cord; *s*, stomach; *s.e*, stone canal; *sph*, sphaeridia; *sp*, spine; *st*, Stewart's organ; *tb*, tubercle; *v*, Polian vesicle on circumoesophageal vessel.

The water-vascular system round the peristome of an irregular Echinoid is shown in Fig. XLIV. The water-vascular ring (*w.v.r*) lies above the peristomial membrane, and just above the circumoesophageal nerve ring, which can be seen in the figure, connecting the five ambulacral nerve cords (*am.n*).

The walls of the podia are strengthened by calcareous spicules, and expand at the end into a sucker. The function of the tube-feet is to help in locomotion. The sucker is pressed against a smooth surface; water from the reservoir or ampulla is driven into the podion, and the tube-foot is thus rendered tense and rigid. The rosette of plates in the sucker is pulled backward, when a vacuum is left between the sucker and the surface against which it is pressed. Firm attachment is thus secured, and the animal can drag itself along (for action, see Fig. XLII.). So powerful are these suckers that, by their means, the Echinoids of the genus *Colobocentrotus* (Fig. XXXIV.) can cling to exposed rock surfaces, fully exposed to the surf of a coral reef.

The supply of water to the water-vascular system is introduced by a membranous vessel—the stone-canal (*s.e*)—which rises from the circumoesophageal ring, and is attached to the plate of the apical system which bears the madreporite (*m*). As we have seen, this plate is perforated by many small pores, through which water can pass into the stone-canal. Owing to the small size of the pores, the water is filtered as it enters. In *Echinus esculentus* the stone-canal is membranous, and the name therefore appears inappropriate. The name was first applied to this canal in the genus *Cidaris*, in which it is hard and calcareous. The flow of water in the interior is regulated by five "Polian vesicles," situated on the circumoesophageal ring, and acting as reservoirs. The latest account of the function of these vessels is given by Uexküll (82).

The main points in the distribution of the water-vascular vessel can be easily verified; but the Blood-vascular or haemal System is more obscure. The most important structure is an ovoid body (Fig. VII. *d.o*), situated beside the stone-canal; it is known as the "dorsal or axial organ," and by other names (see Chapter VIII. pp. 23, 25). Its canal joins above with the stone-canal; it is said to open to the exterior through the madreporite, but this is denied by some authorities (as Hamann). Round the upper end of the "canal of the dorsal organ" is a circular canal known as the "genital ring," which appears to be connected with a series of haemal vessels or lacunae which surround the dorsal organ. In this case it must be also connected with a ring round the oesophagus, from which five branches pass downward beside the pharynx, and then run up along the test below the ambulacra. The "circumoesophageal haemal vessel" is connected with a haemal vessel which runs along the inner side of the stomach.

A third group of canals or vessels consists of a circular sinus round the oesophagus, from which five branches run up the ambulacra between the radial water-vascular vessels and the radial nerve cords. This group of sinuses is known as the "pseudhaemal system."

The function of the haemal and pseudhaemal systems has been much debated, and the relations of their various members are still uncertain. The dorsal organ is sometimes said to be a kidney, as by Hamann (38) and the Sarasins (72). Hartog (39) has supported this by claiming that the circulation is outward through the madreporite; but Cuénot and Ludwig (62) maintain that the current is inhalent. Leipoldt and Prouho (70) point to the absence of any glandular epithelium and of any connection between the cavity of the organ and the general body-cavity. They therefore deny that the organ is a gland, and regard its function as the making of amoeboid cells for the perivisceral fluid. It therefore seems most probable that the haemal system distributes nutrient material through the body, both in solution and by corpuscles (see also Durham, 11 of previous list, p. 36).

A third circumoesophageal ring is that of the Nervous System (Fig. VII. *n.r*). This is placed below the water-vascular ring. From it five radial nerve cords (*r.n.c*), the ambulacral nerves, pass up the inside of the test, between it and the ambulacral water-vascular vessel. Branches from the ambulacral nerve cord pass right and left to the ampullae, and give off smaller branches which pass through the pores to the suckers (Fig. VIII.). The branches fork, one half running up the podion and the other expanding over the surface of the test as a plexus, which controls the movements of the spines and the pedicellariae. A small nerve ring (*n.sp*) surrounds the base of each spine.

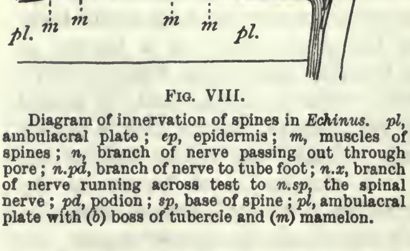


FIG. VIII.

Diagram of innervation of spines in *Echinus*. *pl*, ambulacral plate; *ep*, epidermis; *m*, muscles of spines; *n*, branch of nerve passing out through pore; *n.pd*, branch of nerve to tube foot; *n.x*, branch of nerve running across test to *n.sp*, the spinal nerve; *pd*, podion; *sp*, base of spine; *pl*, ambulacral plate with (*b*) boss of tubercle and (*m*) mamelon.

The Generative Organs are large and simple. They consist of five branching glands (Fig. VII. *g*), which lie attached to the interambulacral plates in the upper part of the body-cavity. Each of the five organs opens to the exterior by a single tube which passes through the pore in a genital plate. The young of *Echinus* are free-swimming plutei, and undergo a metamorphosis during the development and resorption of the pluteal skeleton and its appendages (cf. development of *Echinocyamus*, Chapter VIII. pp. 15-17).

Respiration is largely effected by the aeration of water in the podia; but in addition to this there is a series of five pairs of small folded branchiae or gills (Fig. VII. *b*) lying on the margins of the peristomial membrane. These are diverticula from the general body-cavity, and pass out by the ten notches in the peristomial margin of the test. There are, moreover, five large internal vesicles rising from the upper edge of the masticatory apparatus; these are known as "Stewart's organs" (Fig. VII. *st*), and may act as internal gills.

The ordinary *Echinus*, then, has the following characters:—It consists of a skeleton, which is mostly external, and is composed of numerous closely fitting polygonal plates, bearing spines. Within, it has a simple, coiled, alimentary canal, with mouth and anus at the opposite poles; it has five generative glands; an elaborate series of water-vascular vessels, provided with podia, ending in suckers. This water-vascular system, the blood-vascular system, and the nervous system each consist essentially of a ring round the mouth, from which five branches pass outward, one up the inside of each ambulacrum.

Among the Echinoids the **Variations in Structure** from this simple type are very diverse. Thus the form, instead of being globular, may be depressed into a thin, flat sheet, in which the wide, low roof has to be supported by pillars, as in *Scutella* (Fig. XXXV. 4). In some of these thin forms the posterior margin of the test is lobed and digitate, as in *Rotula* (Fig. IX.); in some cases the ends of the processes unite, leaving perforations or "lunules." In such depressed forms, owing to the sharp division of the test into upper and lower halves, the central podia of the former are useless for purposes of locomotion, and are specialised to serve as branchiae; thus the ambulacra become modified into petaloid and extra-petaloid portions. The ejection of the excreta through an anus situated in the middle of these branchiae would be disadvantageous, owing to the consequent pollution of the water. Hence, in such forms, the anus has passed backwards, and opens in the hinder part of the test. This backward movement of the anus is usually balanced by the forward movement of the mouth, and thus the Echinoid loses its quinqueradiate symmetry and becomes bilaterally symmetrical.

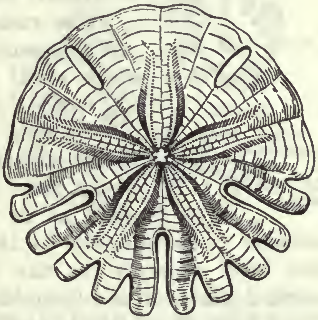


FIG. IX.

Rotula Augusti, with posterior "digitations" and a pair of anterior "lunules."

This change affects not only the position of the external apertures, but the development of the internal organs. Owing to the invasion of the posterior interradius by the anus, the generative gonad there aborts; the gonads thus occur as two lateral pairs, and increase the bilateral symmetry of the Echinoid. This is further strengthened by changes in the structure of the apical system of plates. This system, as in *Cidaris* or *Echinus* (Fig. I.), consists of a double circle of plates. The inner circle is formed by the five genital plates, which are often called the basals. As the latter name has been given to them on the ground that they are the homologues of the basal plates in Crinoids, the older name of genitals is here retained. The outer circle of plates occur in the angles between the genitals, and as they bear the "oculi," they are called the oculars; they have in turn been regarded as homologous with the radial plates of the Crinoid cup and called "radials," while Cuénot, on a different theory of homology, calls them the "terminals." As the double circle of plates surrounds the anus, this form of apical system is known as "endocyclic." From its typical arrangement, as seen in *Cidaris*, variation takes place in two directions. The extreme of one line is seen in *Tiarechinus* (Fig. XVIII.) and *Lysechinus*, in which the apical system of plates forms either half or nearly the whole of the test. In the other direction the plates become less important; in *Aspidodiadema* (Fig. XXII.) they form a single ring of ten plates; and in *Asthenosoma* (Fig. X.) they are either reduced to ten rudimentary plates of no functional importance, or are altogether absent.

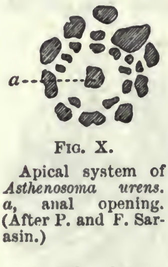


Fig. X.

Apical system of *Asthenosoma urens*. *a*, anal opening. (After P. and F. Sarasin.)

The membrane which lies between the anus and the genital plates is generally covered by numerous small plates, known as the "anal plates." In some genera, such as *Acrosalenia*, some of the anal plates are large and thick, and are firmly attached to the genitals. One of these plates may increase at the expense of the rest, until, as in the genus *Salenia*, there is one large suranal plate attached to the genitals (Fig. XIX.). This plate has been regarded as the homologue of the imaginary dorsocentral plate of the Crinoids. This plate pushes the anus backward from its originally central position.

A tendency towards the retrogression of the anus is shown in all groups of Echinoids. One of its effects is the pulling out of the posterior plates of the apical system, and the consolidation and increase of those in front. Thus in *Zeuglopleurus* the anterior genitals meet along the middle line, while the posterior genitals become narrow and are completely separated from one another by the oculars. In *Pygaster* (Fig. XI. 1) the retrogression has become so marked that the anus lies just outside the apical system, which is therefore "exocyclic." In *Clypeus* (Fig. XI. 2, 3) the anus becomes completely detached from the apical system, which is no longer a ring of plates, but a compact group.

In *Echinus* the madreporite (Fig. I. *m*), or the opening of the water-vascular system, is on the right anterior genital plate. After the anus has receded from the apical system, the madreporite begins to follow it. In a simple compact apical system the pores of the water-vascular aperture occur only in the right anterior corner of the system. Such a system is said to be "ethmophract," as in *Discoidea* or *Micraster* (Fig. XI. 4). In more advanced forms the pores and the plate on which they open extend backward until they separate the two postero-lateral genitals, as in *Spatangus purpureus* (Fig. XI. 5). Such an apical system is said to be "ethmolysian."

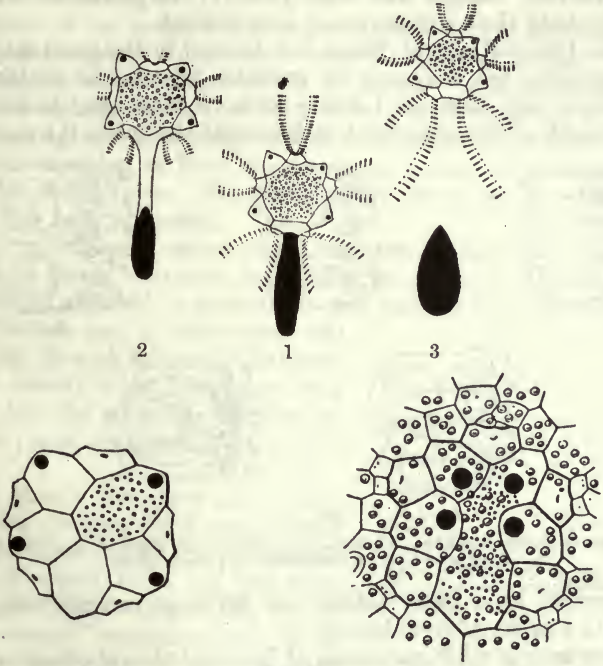


Fig. XI.

Apical systems of Echinoidea. 1, *Pygaster umbrella*; 2, *Clypeus sinuatus*; 3, *Clypeus Hugi*; 4, *Discoidea conica*; 5, *Spatangus purpureus*. In 1 and 2 the anus is still in contact with the apical system; in 3 it is free; 4 is ethmophract, and 5 ethmolysian.

Another change in the apical system is wrought by the elongation of the test in the antero-posterior direction, whereby the apical system becomes elongated. The plates of the two pairs of genitals become adjacent, and completely separate the anterior and the two pairs of oculars from each other; the three anterior ambulacra usually meet close together, and are separated from the two posterior ambulacra by a wide space. The three anterior ambulacra then form the "trivium," and the two posterior form the "bivium." This may be clearly seen in the common Chalk Echinoid, *Echinocorys scutatus*, Leske (syn. *Ananchytes ovatus*, Lam.), (Fig. XXXV. 2). In some cases the separation of the trivium and bivium becomes greater; it is finally completed in the Jurassic genus *Collyrites*, and the living genus *Pourtalesia*, in which the apical system is broken up into two parts, separated by a zone of ordinary interambulacral plates.

Important changes also take place in the plates of the test, affecting both their structure and arrangement.

The Interambulacral Plates are biserial in the great majority of Echinoidea, but they may be uniserial, triserial, or multiserial. Each plate may bear one tubercle or more than one; to increase the strength of the muscular attachment of the spine, the mamelon is perforated by a small hollow, and the boss becomes irregular, owing to a series of crenulations.

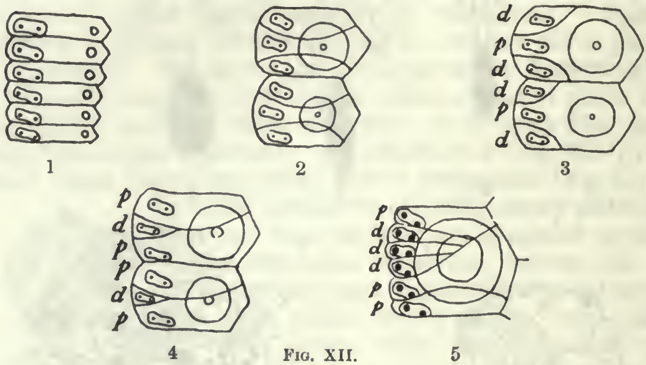


Fig. XII.

Types of ambulacral plates. 1, cidaroid; 2, diademoid; 3, arbacioid; 4, echinoid; 5, cyphosomoid. *d*, demiplates; *p*, primary plates.

Thus among other variations of interambulacral plates are the following:—Those which are unituberculate with the tubercles either plain or crenulate, perforate or imperforate; those which are bi- or multi-tuberculate, and have the tubercles either perforate or imperforate; those which are granulate, as in *Palœechinus;* those which have their edges bevelled, as in *Echinothuria.*

The principal variation in the Ambulacral Plates is in the number of elementary plates (shown by the number of pore-pairs) in a compound plate. There are five main types:—

1. The *cidaroid*, when all the plates are low, simple primaries, as in the Cidaridae, Orthopsinae (Fig. XII. 1).

2. The *diademoid*, when all the plates are primaries, but they are united in sets of threes into compound plates (Fig. XII. 2).

3. The *arbacioid*, when the compound plates are formed of three simple plates, the middle one being a large primary, while the other two are small demi-plates (Fig. XII. 3).

4. The *echinoid*, when the compound plates are formed of three simple plates, but the middle plate is a small demi-plate, and the two others are primaries (Fig. XII. 4).

5. The *cyphosomoid* type, when the compound plates are formed of many simple plates arranged in arcs, in which the middle components are demi-plates (Fig. XII. 5).

In most of the compound ambulacral plates, one or more of the constituents become "demi-plates" by losing their contact with the vertical suture on either side of the series. In some Echinoids some of the plates are further reduced by growth-pressure, so that they lie along the horizontal sutures between the primaries, as in the Echinothuridae, or form broad areas of numerous small plates, as in the Melonitidae. For these plates the name of "klasma-plates" has been suggested.

One important variation affects both the ambulacral and interambulacral plates. In some forms, such as *Asthenosoma*, the plates are thin and attached to powerful lateral muscles (Fig. XXX.), by which the test can be contracted and expanded. In such Echinoids the plates are not closely fitted like stones in a mosaic, but the edges are bevelled, so that the plates overlap like slates on a roof.

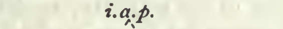


FIG. XIII.

Types of perignathic girdles. 1, disconnected type of *Cidaris*; 2, disconnected type of *Salenia*; 3, simple arch of *Diadema*; 4, capped arch of *Echinometra*. *a*, ambulacral plates; *aur*, auricle; *c*, cap; *i*, interambulacral plates; *i.a.p*, interambulacral processes.

The Mouth Armature also undergoes great changes, which may be best seen by the nature of the perignathic girdle, of which there are five main types. In *Cidaris* (Fig. XIII. 1) it is "disconnected," consisting only of an erect "ridge" situated on the interradial plates around the peristome. In *Salenia* (Fig. XIII. 2), in addition to the ridge, there are small "processes" on either side of the ridge—the processes arise from the ambulacral plates. In the Diadematidae and Echinidae (Fig. XIII. 3) the ridge becomes insignificant and the processes important; they lengthen and form an arch across the ambulacra. The perignathic girdle is then said to be "continuous." The extreme form is met with in such genera as *Echinometra* (Fig. XIII. 4), where the arch is strengthened by a strong cap. In those Echinoids in which the apical system is exocyclic, the jaws become less important. In the Clypeasters the jaws are massive, but their power of movement slight, as they are poised on small vertical processes which fit into a socket on the pyramids.

In the Holectypina we see a gradual reduction of the perignathic girdle, the processes becoming low and the ridge important (as in *Discoidea*), until in *Galerites* the ambulacral processes are absent, and there are only five low interradial thickenings which act as ridges. Finally, from the Atelostomata the perignathic girdle and jaws are completely absent.

The Generative Glands are fairly constant in character, but their number varies, one or more being lost in many Irregular Echinoids. The young are generally free-swimming plutei, but some species are viviparous, the young being nursed in marsupial depressions (Fig. XLIII., see Wyv. Thomson, 81).

In spite of these great variations in structure there are several characters common to all Echinoids. By the selection of those structures which are found in all the Echinoids (except when they have been lost by obviously secondary modification) it is possible to conceive a schematic Echinoid. This is useful, as it helps us to an idea of the primitive ancestor of the class, and as it brings into prominence the features which separate the Echinoidea from the other Echinoderma.

The Primitive Echinoid—for which various names have been suggested—probably had a globular muscular body, covered by an irregular series of polygonal plates. It must have had a simple alimentary canal rising from a mouth situated at the centre of the lower surface; at first, possibly, it may not have had an anus, which, when it came, opened on the upper surface. Three rings surrounded the oesophagus, and from each ring five branches passed up the test to the aboral pole. These three rings with their branches formed the water-vascular, blood-vascular, and nervous systems. Branches from the radial vessels of the water-vascular system passed between the plates of the skeleton to the exterior and acted as suckers. The suckers, by absorption of parts of the plates, at length passed out through pores, instead of through the sutures. The perforated plates were therefore marked off from the others and formed the five ambulacra, while the imperforate plates between constituted the interambulacra. A tube connected the water-vascular ring with the exterior, and allowed the entrance of the necessary water by a single pore. Five unpaired gonads occupied the interambulacral areas. The primitive Echinoid did not have either a stalk, apical system of plates, masticatory apparatus, or perignathic girdle.

Such an animal would have been regarded as an Echinoid, as it was not attached by the aboral surface, but on the contrary had the mouth downwards; as its gonads were quinqueradiate; and as its ambulacra extended from the peristome almost to the aboral pole. The union of these three characters separates the Echinoidea from the rest of the Echinoderma.

Proceeding to discuss the Sub-Classes, Orders, and Families of the Sea-urchins, we may sum up their common characters in the following:—

Diagnosis of the Class.[1]—The Echinoidea are eleutherozoic Echinoderma which are actinogonidial (*i.e.* having the gonads quinqueradiate) and zygopodous (the podia extending from the peristome to near the aboral pole). The body is covered by numerous series of plates, usually polygonal and in vertical series. The apical system may be absent, rudimentary, well developed, or very extensive. The gonads are unpaired and interradial. The body is spherical, or flat, or bilaterally symmetrical, and is covered by spines which may be long, stout, and strong, or present every stage of reduction to such as are fine and silky. An anus is always present, but its position is variable; but it is either at the aboral pole or in the posterior interradius. Respiration is partly by gills and partly by podia. Development is either direct or indirect.

The usual primary subdivision of the Echinoidea is into two sub-classes—PALÆECHINOIDEA and EUECHINOIDEA; the former including approximately all the Palaeozoic, and the latter all the Neozoic Echinoidea. The last formal attempt to define the two groups was that of Duncan (24, p. 4), which has been accepted by Jackson (41).

Excluding from Duncan's diagnoses characters common to the two sub-classes, we find that the only distinction between them is that the Palæechinoidea have either one or more than two vertical rows of plates in each interambulacrum, and two or more vertical rows of plates in each ambulacrum; while the Euechinoidea have two vertical rows of plates in each interambulacrum and in each ambulacrum.

This classification is open to two fatal objections. The rule is not absolute. Thus in the Cretaceous genus *Tetracidaris* there are four rows of plates in each interambulacrum; and in such genera as the Euechinoid *Tripneustes*, it is no more correct to say that there are only two rows of vertical plates in the ambulacra, than it would be to say so of the Palæechinid *Palæechinus* which is described as having more than two vertical series. In the second place, the classification separates fairly close allies, and brings together extremely divergent forms. Thus, such a species as the Liassic Euechinoid *Cidaris edwardsi* is far more closely allied to such a Palæechinoid as *Archaeocidaris* than the latter is allied to *Tiarechinus.*

The separation of these two sub-classes was originally based on several very definite characters, such as the imbrication of the plates, the flexibility of the test, and the number of pores in the genital plates. One by one these characters have been shown to be valueless for the purpose for which they were used, but the classification based on them has been retained. It is preferable to return to the division of the Echinoidea into —REGULARIA and IRREGULARIA.

---

[1] Emended from Bell (10), p. 214.

SUB-CLASS 1. REGULARIA ENDOBRANCHIATA.

Mouth and anus at opposite poles. Anus surrounded by the apical system of plates, when they are present. No external gills.

ORDER 1. **Bothriocidaroida,** Schmidt.

Lovén has shown that in many young Echinoids the interambulacrum begins and ends with a single plate. In the oldest known Echinoids the whole interambulacrum consists of a single vertical series. The Echinoids in question are two species from the Ordovician rocks of Esthonia. They belong to the genus *Bothriocidaris*, Schmidt.

Bothriocidaris has a small test, on the top of which is an apical system (Fig. XIV. 2), composed of a ring of five large ocular plates, in the angles between which are five small imperforate genital plates. Each ocular plate has two pores. The anus is in the centre of the apical system, and the periproct is covered by six or eight anal plates. The test is mainly formed by the ambulacra. Each ambulacrum consists of two vertical series of hexagonal plates, each perforated by one or two pore-pairs. The interambulacra are narrower than the ambulacra, and consist of a single series of plates which do not extend to the peristome, from which they are cut off by the expansion of the peristomial ambulacral plates (Fig. XIV. 3). The most recent description of the genus is by Jaekel (42).

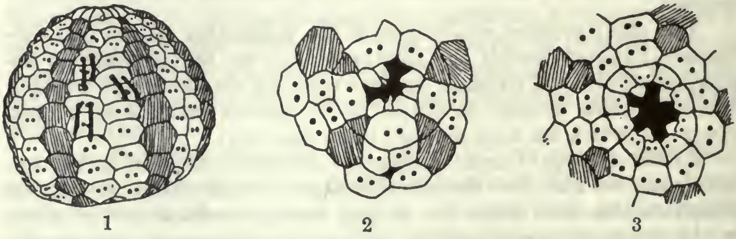


FIG. XIV.

Bothriocidaris Pahleni, Schmidt; Ordovician, Russia. 1, from the side; 2, apical system; 3, peristomial plates. The interambulacral plates are shaded.

ORDER 2. **Cystocidaroida,** Zittel.

Echinoidea Regularia Endobranchiata with test ovoid, flexible. No apical system of plates. Madreporite and anus (when present) open independently in the posterior interambulacrum. Mouth central. Ambulacra of low, closely packed plates. Interambulacra broad, of numerous, thin, and irregularly arranged plates, bearing short spines. A masticatory apparatus present.

FAMILY 1. PALAEODISCIDAE. Cystocidaroida with depressed, discoid body. The ambulacral plates are biserial, crowded, and narrow; on the oral surface they are not perforated by pores, but the podia pass out through the sutures between the plates. Near the aboral pole the ambulacra are narrower and pores occur in the plates. Genus—*Palaeodiscus*, Salter, from the Silurian of Ludlow. It is the most primitive of known Echinoids and has been frequently assigned to the Stelleroida. The main radial water-vascular vessels appear, however, to have passed along the inside of the test instead of below or outside the ambulacral plates, as in Stelleroids (Salter, 42 on p. 280, *ante;* Neumayr, 64 ; Gregory, 36).

FAMILY 2. ECHINOCYSTIDAE. Cystocidaroida, in which the ambulacra consist of narrow plates, each perforated by a pore-pair. The pore-pairs are biserial ; most of the plates are low primaries, but demi-plates also occur. Genus—*Echinocystis*, Wyv. Thoms. (*non* Hall), Silurian ; one of the most remarkable of known Echinoids. It has no apical system of plates, and the anus and madreporite both open independently in the posterior interradius. The genus is therefore sometimes described as exocyclic, but it is really acyclic (Gregory, 36).

ORDER 3. **Cidaroida.**

Echinoidea Regularia Endobranchiata, in which the peristome is central ; the periproct is central on the aboral surface of the body, and is surrounded by the apical system of plates. The ambulacra each consist of two vertical series of simple narrow plates, some of which may be demi-plates. The interambulacral plates are unituberculate, bearing large spines. There is a dental apparatus.

In the Devonian system the Echinoids are scarce, but their characters indicate a marked advance upon the Silurian species in the strength of the tests, owing to the greater thickness and regularity of the plates. Two main lines of differentiation are apparent. In the first the increase takes place in the interambulacral plates, in the second the ambulacral plates become more important. The former is the order Cidaroida, the latter is the order Melonitoida.

There are four families of Cidaroida, of which three are extinct. The most typical genus is *Cidaris;* the earliest and most primitive is *Lepidocentrus.*

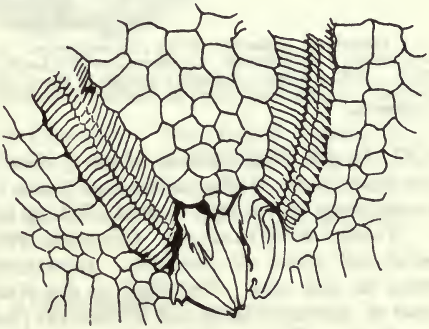


FIG. XV.
Diagram of arrangement of plates near peristome in *Lepidocentrus.* Devonian, Germany.

FAMILY 1. LEPIDOCENTRIDAE. Cidaroida with ambulacral pore-pairs in a single series. Interambulacral plates in more than two vertical rows. Test flexible, owing to imbrication of the plates. No interambulacral plates pass on to the peristomial membrane. This family is represented by four Palaeozoic genera—*Lepidocentrus*, Müller, Devonian ; *Lepidechinus*, Hall, Devonian and Lower Carboniferous; *Koninckocidaris*, Dollo & Buisseret, and *Perischodomus*, M'Coy, both Carboniferous. The main character of the family is that none of the interambulacral plates occur detached from the test on the peristomial membrane (Fig. XV.).[1]

Family 2. Archaeocidaridae. Cidaroida with ambulacral pore-pairs in a single series. Interambulacral plates in more than two vertical rows. Test slightly flexible, owing to slight imbrication of plates. Peristome large, several rows of the interambulacral plates as well as of the ambulacral passing on to the peristomial membrane. The main character of this family is that, while the interambulacral plates remain in more than two series and somewhat imbricated, in both of which features it agrees with the *Lepidocentridae*, it has acquired the peristomial characters of the true *Cidaridae*. Genera—*Archaeocidaris*, M'Coy (Fig. XVI. 2), and *Lepidocidaris*, Meek & Worthen, both Carboniferous. In the latter some of the ambulacral plates are demi-plates. *Xenocidaris*, known from spines only, may also belong here.

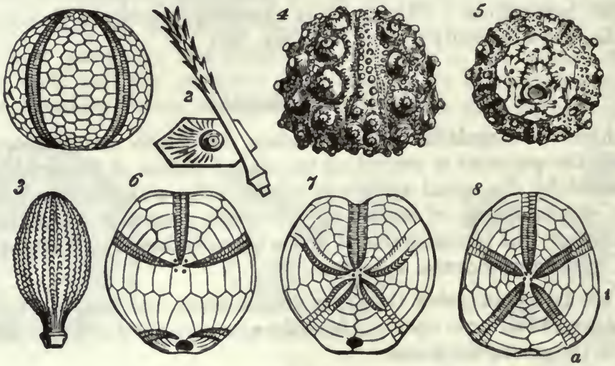


Fig. XVI.

1, Palæechinus sphaericus, M'Coy; Carboniferous. *2*, A plate and spine of *Archaeocidaris urii*, Flem.; Carboniferous. *3, Cidaris glandifera*, Goldf.; Jurassic. *4, Hemicidaris intermedia*, Flem.; Mid. Jurassic. *5, Salenia petalifera*, Desm.; Cretaceous. *6, Dysaster ringens*, Ag.; Jurassic. *7, Enallaster Greenovi*, Forbes; Cretaceous. *8, Catopygus columbarius*, Lam.; Cretaceous.

Family 3. Cidaridae. Cidaroida with ambulacral pore-pairs uniserial and plates all primaries. Interambulacral plates in two vertical series in each area. Test rigid, as the plates do not imbricate. Several rows of interambulacral and ambulacral plates pass on to the peristomial membrane. The family includes the living genus *Cidaris*, Leske, with its numerous subdivisions—*Rhabdocidaris*, *Chondrocidaris*, *Stereocidaris*, *Discocidaris*, *Tylocidaris*, *Typocidaris*, *Dorocidaris*, etc. *Goniocidaris*, Des.; *Orthocidaris*, Cott.; *Temnocidaris*, Cott.; *Polycidaris*, Quenst., are also genera of this family. *Cidaris* is one of the most primitive of recent Echinoids, and therefore one of the most instructive.

---

[1] The systematic value of this character is shown in Jackson's interesting paper (41).

Fig. XVII. gives the aboral surface of *Cidaris* (*Stereocidaris*) *subvesiculosa*, from the Chalk, showing its primitive dicyclic apical system; its massive interambulacral plates separated by very narrow ambulacra, composed only of low, simple primaries (Fig. XII. 1). The arrangement of the peristomial plates in this genus is very important; the peristomial membrane is covered by loose plates which include representatives of both the ambulacral and interambulacral series. There are no arched processes over the ambulacra, the perignathic girdle consisting only of interradial ridges (Fig. XIII. 1). The internal gills,[1] or Stewart's organs, are well developed.

FAMILY 4. DIPLOCIDARIDAE. Cidaroida with ambulacral pore-pairs biserial. Interambulacral plates in two or more vertical series in each area. Peristomial plates as in Cidaridae. This family includes the interesting genus *Tetracidaris*, Cotteau, which has four rows of plates in each interambulacrum. This Palæechinoid character is associated with a type of ambulacrum which, for the Cidaridae, is remarkably specialised. A second genus is *Diplocidaris*, Desor.

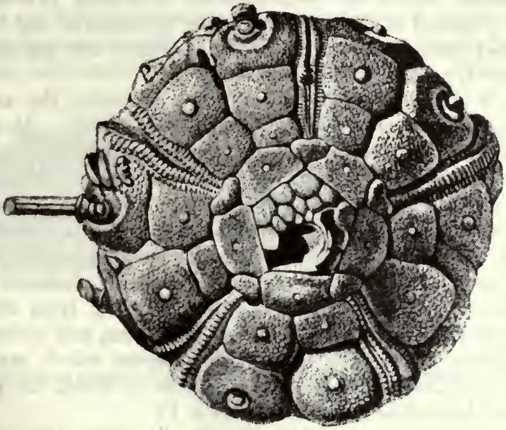


FIG. XVII.
Cidaris (Stereocidaris) subvesiculosa, d'Orbigny; from the Chalk.

ORDER 4. Melonitoida.

Echinoidea Regularia Endobranchiata, in which the peristome is central on the lower surface, and the periproct central on the upper surface, surrounded by the apical system of plates. The ambulacra each consist of two or more rows of simple plates, of which some or all may be demi-plates, or klasma-plates. The interambulacral plates are covered by granules bearing short, simple spines; but occasional tubercles may occur.

---

[1] It should be remembered that the respiratory function of these organs is still hypothetical.

There are more than two vertical series in each interambulacrum. There is a masticatory apparatus, but no external gills. The order is therefore endocyclic, gnathostomate, anectobranchiate, with simple ambulacral plates, and having granulate interambulacrals.

This order represents an offshoot from the main Cidarid stem. It began in the Silurian, attained its maximum in the Carboniferous, and became extinct in the Permian. There are three families in the order, and these form an evolutionary series. All differ from the Cidaroida, by having granular instead of unituberculate plates, which, by itself, however, is not a character of ordinal importance. The main feature is the great increase in the importance of the ambulacral areas, reminding us of *Bothriocidaris.* This character is well developed in the two more specialised families, but in the Palæechinidae it is only just appearing. Thus the family named is closely allied to the members of the Cidaroida, and is separated from that order only as it marks the beginning of a very remarkable type of Echinoid structure.

FAMILY 1. PALÆECHINIDAE. Melonitoida, in which the ambulacral plates are essentially biserial (or in one case triserial). Most of the plates are primaries, and the remainder long, narrow, demi-plates. The plates of the test are rigidly attached. One row of interambulacral plates passes on to the peristomial membrane. Genera—*Palæechinus,* M'Coy (pars), and *Rhoëchinus*, Keeping; and perhaps also *Perischocidaris*, Neumayr (syn. *Homotoechus*, Sollas). The family is separated from the Melonitidae, owing to the great difference in the characters of the ambulacra; but it is regarded as the ancestral group from which that family was derived. *Rhoëchinus* is the simplest genus, and includes those with the pore-pairs in a single series. *Palæechinus,* which ranges from the Silurian to the Carboniferous, includes those in which the pore-pairs are biserial, and demi-plates occur (Fig. XVI. 1).

FAMILY 2. MELONITIDAE. Melonitoida, in which the ambulacral plates are all small, simple klasma-plates, which are multiserial in arrangement. These form broad areas. The test is rigid. One row of interambulacral plates passes on to the peristomial membrane. This family represents a marked advance on the previous one. The tendency towards the crowding of the ambulacral plates and the reduction of many of them into klasma-plates has made great progress. Genera—*Oligoporus*, Meek & Worthen, Carboniferous; the plates agree in general character with those of *Palæechinus*, but the ambulacral plates are quadriserial instead of biserial. *Melonites*, Norwood & Owen, Carboniferous; the process has gone further, and each ambulacrum consists of from six to sixteen vertical series.

FAMILY 3. LEPIDESTHIDAE. Melonitoida, in which the ambulacral plates are small klasma-plates, multiserial in arrangement. The plates of the test imbricate. None of the interambulacral plates pass on to the peristomial membrane. This family is the extreme type of the Melonitoida, and represents a condition in which the plate arrangement becomes most irregular. It includes the species with the greatest number of plates in the ambulacra. The plates being thin and small, the test is necessarily fragile, a danger to the animal obviated by the imbrication of the plates.

As is the rule among all thin-plated, flexible Echinoids, there is a marked tendency to irregularity, especially shown in *Pholidocidaris.* Genera—*Pholidocidaris* and *Lepidesthes*, both of Meek & Worthen, from the Lower Carboniferous.

ORDER 5. **Plesiocidaroida**, Duncan.

Echinoidea Regularia Endobranchiata with a small rigid test, peristome and periproct central and opposite. Periproct in the centre of an apical system of large plates, which forms half of the whole test. The ambulacral areas are short and biserial. Their plates are all simple primaries. The interambulacra have each a single peristomial plate.

FAMILY 1. TIARECHINIDAE. Plesiocidaroida with desmactinic ambulacra (*i.e.* ambulacra continuous from peristome to apical system). Each interambulacrum consists of four plates, viz. a single peristomial plate and three tall, vertical plates in a horizontal row. Genus—*Tiarechinus,* Neumayr; Trias, Tyrol. The figures (Fig. XVIII.) show its enormous apical disc, small ambulacra, and vertical interambulacral plates.

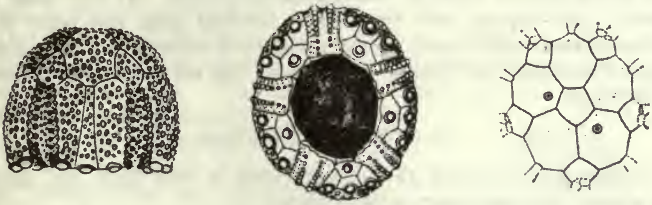

1 2 3

FIG. XVIII.

Tiarechinus princeps, Neumayr; Trias, Tyrol. 1, from the side; 2, from below; 3, the apical system (magnified).

FAMILY 2. LYSECHINIDAE. Plesiocidaroida with ambulacra limited to grooves on lower surface of the test. Each interambulacrum begins with a single peristomial plate succeeded by a row of two plates, and this by one or more containing three plates. Genus—*Lysechinus*, Greg. (**34**); Trias, Tyrol.

This small order includes the two most aberrant of all known Echinoids. In *Tiarechinus* there are three vertical plates in each interambulacrum, while the calyx is much larger and more crinoidal in aspect than in any other Echinoid. It has hence been regarded as an argument in favour of the origin of the Echinoidea from an ancestor in which the apical system was of great importance. Both known genera of Plesiocidaroida are small forms, and they appear to have lived under unfavourable conditions in Triassic lagoons, for the Echinoids with which they are associated are all dwarfed. Hence it seems more natural to dismiss *Tiarechinus* and *Lysechinus* as two aberrant genera, in which the test was strengthened by the development of the apical plates. Thus they have no bearing on the character of the ancestral Echinoid.

Sub-Class 2. Regularia Ectobranchiata.

Echinoidea with mouth and anus at opposite poles. Endocyclic, with external gills.

Order 1. **Diademoida,** Duncan.

Echinoidea Regularia Ectobranchiata in which the mouth and anus are both central and opposite. The anus opens in the centre of the apical system (which may however be rudimentary). The external branchiae pass out through the buccal clefts. A dental apparatus is present. There are no interambulacral plates on the peristomial membrane. The ambulacral plates are generally compound.

This order marks a great advance on any of those previously defined. The ambulacral plates in some forms remain as simple primaries, but in the majority they unite into compound plates, different from anything met with in the preceding groups. At the same time external gills appear, with or without internal gills, and none of the interambulacral plates occur on the peristomial membrane. The order is accepted practically as defined by Duncan,[1] but his method of division is not followed.

Sub-Order 1. Calycina.

Diademoida in which the apical system is very large and includes one or more supplementary suranal plates.

As we have seen in the description of *Tiarechinus* and *Lysechinus*, these small forms gained strength by the development of a series of large apical plates. In one group of the Diademoida the same result is obtained by the incorporation of one or more "suranal plates" in the apical system. Like *Tiarechinus*, the Echinoids in which this feature first appeared are very small. The character has persisted from the Trias to the present time, but the Echinoids in which it occurs are never large.

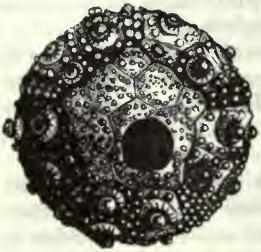


Fig. XIX.
Salenia varispina. Abactinal surface.

Family 1. Saleniidae. Calycina in which the ambulacral plates are simple primaries, and there is one large suranal plate in the apical system. Genera—*Salenia*, Gray; *Heterosalenia*, Cott.; *Peltastes*, L. Ag. (Fig. XVI. 5; Fig. XIX.); *Goniophorus*, L. Ag.; *Baueria*, Ebert.

Family 2. Acrosaleniidae. Calycina in which there are one or more suranal plates in the apical system; the ambulacral plates are simple primaries near the apical system, but compound, with demi-plates near the peristome. Genus—*Acrosalenia*, L. Ag.

---

[1] The perignathic girdle is not always continuous as stated in his diagnosis.—Duncan (24), p. 24.

Sub-Order 2. Arbacina.

Diademoida in which the ambulacral plates are simple primaries near the apical area; at the ambitus they are compound. Some or all of the compound plates consist of a large central primary, on either side of which is a small demi-plate. (These plates are on the "arbacioid" type of Duncan.)

The Echinoids of this sub-order contain forms characterised by remarkable simplicity of structure. The interambulacral plates are large and generally of the Cidarid type. The peristome is large. The ambulacra are narrow except on the ambitus and near the peristome, where they often expand somewhat suddenly. The apical system is large and simple. There are two families, one of which is typically Jurassic, and the other typically Cainozoic. This difference in age has probably delayed the recognition of the resemblances between the two families. There are, however, several Cretaceous genera which link the Jurassic and the Cainozoic forms, and thus support the idea that the Arbaciidae are the descendants of the Hemicidaridae.

Family 1. Hemicidaridae. Arbacina in which the ambulacral plates are narrow, and consist of simple primary plates for some distance from the apex. The compound plates are few in number, and irregular in arrangement; the arbacioid type of plate is not extensively developed, many of the compound plates being diademoid, though with the sutures approaching the arbacioid character (Fig. XX.). This family is not well marked off from the Arbaciidae. It represents the characters of that family imperfectly developed. Genera—*Hemicidaris*, L. Ag. (Fig. XVI. 4; Fig. XX.), is the most important; *Acrocidaris*, L. Ag.; *Goniopygus*, L. Ag.; *Circopeltis*, Pomel; *Cidaropsis*, Cott.; *Glypticus*, L. Ag.; *Leptocidaris*, Quenstedt, and several subgenera.

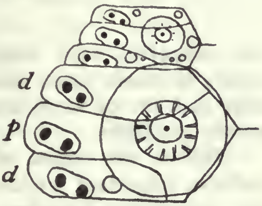


Fig. XX.

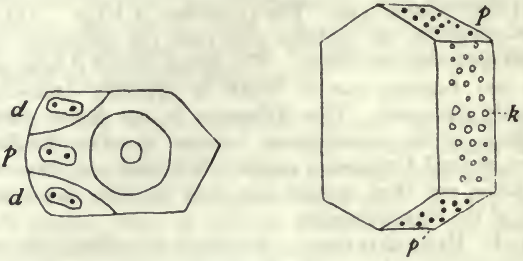
Two compound ambulacral plates of *Hemicidaris intermedia*, Flem.; Jurassic. Showing the arbacioid structure of the plates. (After Duncan.)

Family 2. Arbaciidae. Arbacina with small, generally sub-conical tests. They are ornamented by numerous granules; a bare space occurs in the middle of the upper part of each interambulacrum. The ambulacral plates are mainly on the arbacioid type, but there are some primaries near the apical system, and a few diademoid plates between the primaries and the arbacioid plates. Ocular pores double. This family includes four primitive genera; of these two are only known living, one occurs in the North American Cainozoic, and the fourth ranges from the Eocene to the present day. The main distinctions from the Hemicidaridae are that in the ambulacra there are fewer primaries and more compound plates, and that the union of the interambulacral plates is strengthened by the development of a series of knobs and sockets. These occur on the facets of the plates, the knobs of one plate fitting into the sockets of the next (Fig. XXI. 2).

Genera—*Arbacia*, Gray ; *Echinocidaris*, Dunc. *non* Desmoulins ; *Coelopleurus*, Ag. ; *Podocidaris*, A. Ag.

SUB-ORDER 3. DIADEMINA.

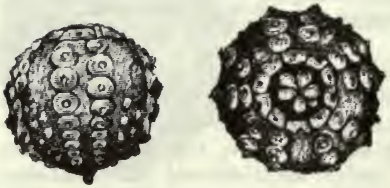
Diademoida including a series of Echinids in which the compound ambulacral plates gradually increase in complexity. In the simplest forms all the plates are simple primaries; in others, some of the plates are compound, each being formed of three primaries (the diademoid type) ; in others, again, some of the plates consist of three or more primaries and one or more demi-plates, which occur between the aboral and middle primaries.



1 FIG. XXI. 2

Arbacia nigra. 1, ambulacral plate ; 2, interambulacral plate showing articular pits (p) and knobs (k).

This is the largest of the sub-orders of regular Echinoidea and includes important families. It represents an evolutionary series from the primitive *Eodiadema* to the complex Cyphosomatidae or the abnormal Echinothuridae. The simplest members of the sub-order cannot be distinguished from the Saleniidae by ambulacral structure alone, but they are clearly separated by the absence in this group of any suranal plate.



1 FIG. XXII. 2

Aspidodiadema tonsum (after A. Agassiz). 1, from the side ; 2, from above showing the apical system composed of a single ring of ten plates.

FAMILY 1. ORTHOPSIDAE. Diademina with the ambulacral plates all simple primaries, and the pore-pairs in a simple series. This interesting family includes a series of simple Echinoids, which form the beginning of the sub-order Diademina. It includes seven genera ranging from the Middle Lias to the present day, viz. *Eodiadema*, Dunc. ; *Archaeodiadema*, Greg. ; *Orthopsis*, Cott. ; *Gymnodiadema*, Lor. ; *Peronia*, Dunc. ; *Echinopsis*, L. Ag. ; *Aspidodiadema*, A. Ag. The only living genus is *Aspidodiadema*, a deep-sea form dredged by the *Challenger*. It has been made the type of a special family by Duncan, but it seems to be a survival of the Orthopsidae. The apical plates form a single circle, within which are five large anal plates around the anus (Fig. XXII.).

Family 2. Diadematidae. Diademina in which the ambulacral plates at the ambitus are compound, and consist of three (Fig. XXIII.) or more (Fig. XXIV.) primaries fused together with an occasional demi-plate (*d*). This family includes fourteen genera ranging from the Lias to recent times, viz. *Diadema*, Gray; *Pseudodiadema*, Desor (Figs. XXIII., XXIV.); *Microdiadema*, Cott.; *Diademopsis*, Desor; *Hemipedina*, Wright; *Echinodiadema*, Cott.; *Pleurodiadema*, Lor.; *Placodiadema*, Dunc. (Fig. XXV.); *Heterodiadema*, Cott.; *Codiopsis*, L. Ag.; *Magnosia*, Mich.; *Cottaldia*, Des.; *Centrostephanus*, Peters; *Helikodiadema*, Gregory.

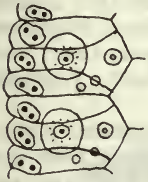


Fig. XXIII.

Compound ambulacral plates of *Pseudodiadema hemisphaerica*; the simple diademoid type of three primaries.

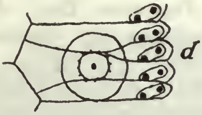


Fig. XXIV.

Compound ambulacral plate of *Pseudodiadema hemisphaerica*, containing a demi-plate (*d*).

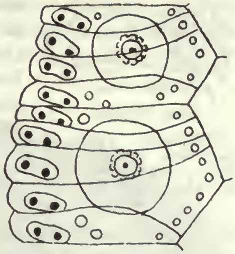


Fig. XXV.

Compound ambulacral plates of *Placodiadema Michelini* (after Duncan); one formed of four and the other of five components.

Family 3. Diplopodiidae. Diademina in which the ambulacral plates are compound; the pore-pairs are biserial either throughout the area, or at least near the peristome (Fig. XXVI.). Genera—*Diplopodia*, M'Coy; *Phymechinus*, Des.; *Asteropsis*, Cott.; *Diplotagma*, Schlüter; *Plistophyma*, Peron & Gauthier; (?) *Acanthechinus*, Duncan & Sladen; *Micropyga*, A. Ag.

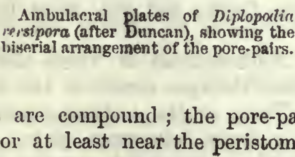


Fig. XXVI.

Ambulacral plates of *Diplopodia versipora* (after Duncan), showing the biserial arrangement of the pore-pairs.

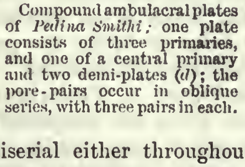


Fig. XXVII.

Compound ambulacral plates of *Pedina Smithi*; one plate consists of three primaries, and one of a central primary and two demi-plates (*d*); the pore-pairs occur in oblique series, with three pairs in each.

Family 4. Pedinidae. Diademina in which the ambulacral plates are compound and the pore-pairs are triserial (Fig. XXVII.). Genera—*Pedina*, Ag.; *Pseudopedina*, Cott.; *Heterocidaris*, Cott.; *Stomechinus*, Des.;

Polycyphus, Ag.; *Pedinothuria*, Greg.; *Micropedina*, Cott.; *Codechinus*, Des.; *Echinopedina*, Cott.; *Echinothrix*, Pet.; *Astropyga*, Gray.

Family 5. Cyphosomatidae. Diademina in which the ambulacral plates are compound; they are high with from three to seven pore-pairs in an arc; the adoral and supra-adoral, and sometimes also the aboral plates are primaries. The remaining constituents are demi-plates (Fig. XXVIII.). Genera—*Actinophyma*, Cott. & Gauth.; *Cyphosoma*, Ag.; *Leiosoma*, Cott. & Triger; *Gauthieria*, Lamb.; *Thylechinus*, Pomel; *Coptosoma*, Des.; *Micropsis*, Cott.; *Orthechinus*, Gauthier (syn. *Gagaria*, Dunc.); *Triplacidia*, Bittner.

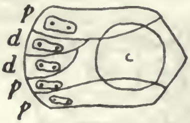


Fig. XXVIII.

Ambulacral plate of *Cyphosoma*, composed of three primaries and two demi-plates.

In the normal compound ambulacral plates of the Diadematidae each plate consists of three primaries; but, as in the case of Fig. XXIV., an extra demi-plate sometimes appears below the uppermost primary. This is the link between the typical Diadematidae and Cyphosomatidae. Demi-plates appear in Diadematids in the Middle Oolites; the Cyphosomatidae begin in the Upper Oolites and attain their maximum in the Cretaceous. The last members of the family lived in the Eocene.

Family 6. Echinothuridae. Diademina in which the test is more or less flexible; the plates are thin and usually separated by membrane. Apical system rudimentary (Fig. X.); ambulacral plates triserial, arranged typically in triplets of a central primary between two klasma-plates. In one genus three triplets unite together to form a single plate. This interesting family was founded by Wyville Thomson to include the Chalk fossil *Echinothuria*, S. P. Woodw., and some living Echinoids dredged by the *Porcupine* Expedition. As the tests are flexible and the plates overlap, the family was at first compared with the Palaeozoic Echinoids. P. and F. Sarasin argued from the rudimentary nature of the apical disc, and from the great size of the "Stewart's organs" and the presence of powerful radial muscles (the two latter characters being very noticeable in a new species of *Asthenosoma* described by those authors) that the Echinothuridae were a primitive family of Echinoids, and helped to establish the origin of this class from a Holothuroid ancestor. Neviani accepted this conclusion. But, as has recently been shown (Gregory, 35), the family is an offshoot from the Pedinidae; the genus *Pedinothuria* helps to bridge the gap between *Pedina* and the oldest known Echinothurid—*Pelanechinus*.

Sub-Family 1. Pelanechininae. Echinothurids of which the ambulacral plates are compound; those near the apex consist of two demi-plates and a large middle primary. Those at the ambitus consist of three sets of three plates united into a single polyporous plate; each triplet of this compound plate consists of a primary between two demi-plates or klasma-plates. Genus—*Pelanechinus*, Keeping; Corallian, Wiltshire. An admirable account of the genus has been given by Groom (37). Sub-Family 2. Echinothurinae. Echinothuridae in which the ambulacral plates are simple and free; they consist of triplets, each composed of a large central primary, and with an isolated klasma-plate above and below it. Genera—*Echinothuria*, S. P. Woodw.; from the Chalk; *Asthenosoma*, Grube (Fig. XXIX.), a living genus with large "Stewart's organs" and powerful radial muscles; and *Phormosoma*, Wyv. Thomson, with rudimentary Stewart's organs and without powerful radial muscles. In the Echinothurinae the reduction in the calcification of the test, which had begun in *Pelanechinus*, has been carried so far, that all the ambulacral plates are disunited, but are held together by strong muscular lining. In *Asthenosoma* there is, in addition, a series of powerful radial muscles (Fig. XXX.), which give a panting motion to the test. The spines are covered by epithelium, and when handled can inflict a sharp sting.

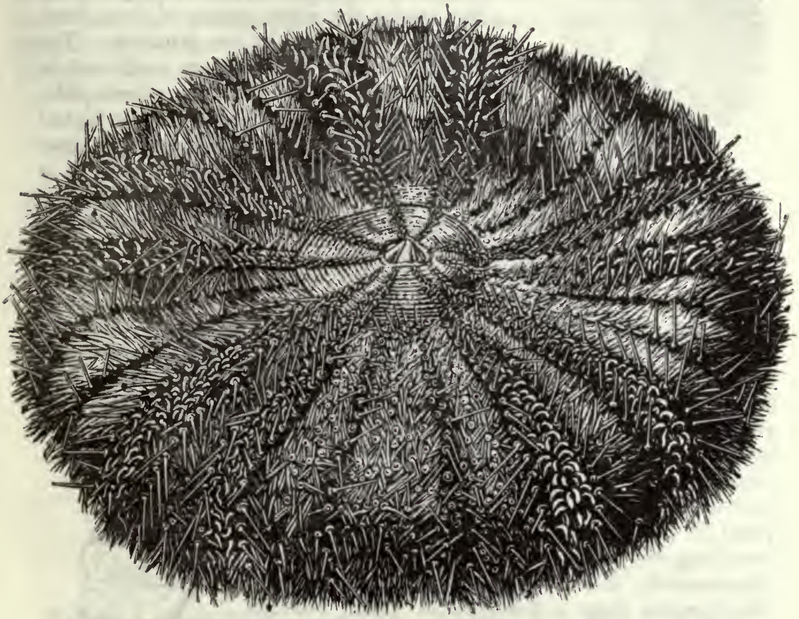


Fig. XXIX.

Asthenosoma hystrix. Oral surface; the tips of the jaws are seen protruding through the peristomial membrane.

Sub-Order 4. Echinina.

Diademoida in which the ambulacral plates typically consist of an aboral and adoral primary, between which are one or more demi-plates. The sub-order includes a series of Echinoids, in the simplest of which the compound ambulacral plates consist of three primaries, and are separated from one another by free primaries.

In the sub-order Arbacina the plates of the test are often fixed together by sockets and knobs (Fig. XXI. 2), while in some genera, such as *Glypticus*, there is a great development of the subsidiary ornament. In the simplest forms of the Echinina both characters are further developed. In the Chalk genera, *Glyphocyphus* and *Zeuglopleurus* (Fig. XXXI.), the sutures are excavated by deep hollows, while the plates are thickened by granules and ridges. From such forms as these there is a gradual transition to others with deep pits, which dowel into the plates, as in *Temnopleurus* (Fig. XXXII.). The transition from the diademine to echinine type of ambulacral plates is shown by *Zeuglopleurus* and *Ortholophus*. In the former the plates consist of three fused primaries, separated by free primaries. The middle primary is often very small, and in *Ortholophus* is often reduced to a demi-plate. The plates then have the arrangement typical of *Echinus*. From this oligoporous plate the polyporous strongylocentrotoid type is produced by the development of one or more demi-plates between the aboral and adoral primaries.

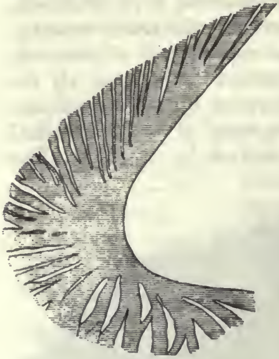


Fig. XXX.
Radial muscle of *Asthenosoma*. (After P. and F. Sarasin.)

This sub-order began in the Cretaceous.

Family 1. Temnopleuridae. Echinina in which the compound ambulacral plates are formed of three constituents. In the oldest and most primitive forms the three plates are all primaries; in the later and more specialised types the middle plate is crowded into a demi-plate (*i.e.* the plates are on the Echinoid type). There is a great development of superficial ornamentation, and the plates are hollowed or undermined by depressions or pits. Sub-Family 1. Glyphocyphinae. Temnopleuridae in which the compound ambulacral plates are composed of three primaries; the plates are united by dowelling, but there are no sutural pits. Genera—*Glyphocyphus*, Haime (syn. *Rhabdopleurus*, Cott.); *Zeuglopleurus*, Greg.; *Echinocyphus*, Cott.; *Paradoxechinus*, Laube; *Leiocyphus*, Cott. Sub-Family 2. Ortholophinae. Temnopleuridae in which the compound ambulacral plates are composed of two primaries and an intermediate demi-plate. The plates are united by dowelling, but there are no sutural pits. Genera —*Ortholophus*, Dunc.; *Coptophyma*, Peron & Gauth.; *Lepidopleurus*, Dunc. & Slad.; (?) *Trigonocidaris*, A. Ag.; *Dictyopleurus*, Dunc. & Slad.; *Arachniopleurus*, Dunc. & Slad. (*Radiocyphus*, Cott.). Sub-Family 3. Temnopleurinae. Temnopleuridae in which the compound ambulacral plates are composed of two primaries and an intermediate demi-plate. True sutural pits occur, and these often undermine the plates (Fig. XXXII.). Genera — *Temnopleurus*, Ag.; *Temnechinus*, Forbes; *Opechinus*, Desor; *Pleurechinus*, Ag.; *Salmacis*, Ag.; *Salma-*

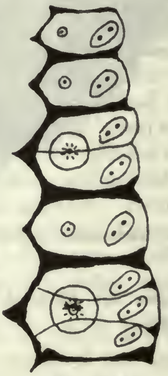


Fig. XXXI.
Zeuglopleurus costulatus, Greg.; plates of upper part of an ambulacrum showing simple and compound plates and grooved sutures.

copsis, Döderlein; *Mespilia*, Desor; *Microcyphus*, Ag.; *Amblypneustes*, Ag.; *Goniopneustes*, Dunc.; (?) *Holopneustes*, Ag.; (?) *Grammechinus*, Dunc. & Slad.

FAMILY 2. TRIPLECHINIDAE. Echinina in which the ambulacral plates consist of two primaries and an intermediate demi-plate. The three pairs of pores are arranged in arcs of triplets; the sutural faces of all plates are smooth; and there are no pits or grooves in their substance; so that in these three respects the Triplechinidae differ from the Temnopleuridae, though an approach to this family is shown by *Grammechinus*. Genera—*Echinus*, Linn.; *Psammechinus*, Ag.; *Micropsina*, Cott.; *Leiopedina*, Cott.; *Tripneustes*, Ag. (= *Hipponoë*); *Stirechinus*, Desor; *Glyptechinus*, Lor.; *Hybechinus*, Desor; *Toxopneustes*, A. Ag.; *Boletia*, Desor; *Evechinus*, Verrill; *Pedinopsis*, Cott.

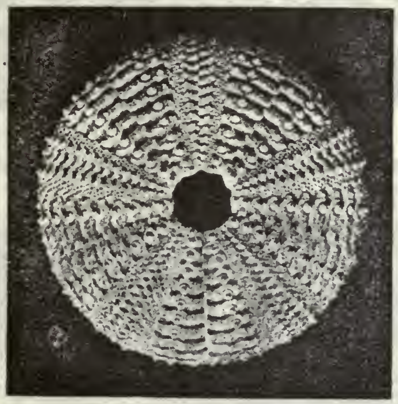


FIG. XXXII.

Temnopleurus toreumaticus (after Agassiz), showing the pitted test.

FAMILY 3. STRONGYLOCENTROTIDAE. Echinina with more than three constituents in each ambulacral plate, the pores being in high curved arcs. Genera—*Strongylocentrotus*, Brandt; *Sphaerechinus*, Desor; *Echinostrephus*, A. Ag.; *Eurypneustes*, Duncan & Sladen; *Pseudoboletia*, Trosch.; *Aeolopneustes*, Dunc. & Slad.

FAMILY 4. ECHINOMETRIDAE. Echinina with three or more constituents in each ambulacral plate. The test is elongate, and the long axis does not coincide with the antero-posterior axis. Genera—*Echinometra*, Gray; *Stomopneustes*, Ag.; *Heterocentrotus* and *Colobocentrotus*, Brandt; *Parasalenia*, A. Ag. The elliptical shape of the test is the most remarkable character in this family. The perignathic girdle is very powerful, each arch being surmounted by a cap (Fig. XIII. 4). The spines are large and very varied in form. In *Heterocentrotus* the secondary spines form a fur below the primary spines (Fig. XXXIII.); in *Colobocentrotus* the spines are stout and end in flat surfaces; they are so crowded together as to form a natural armour-plate (Fig.

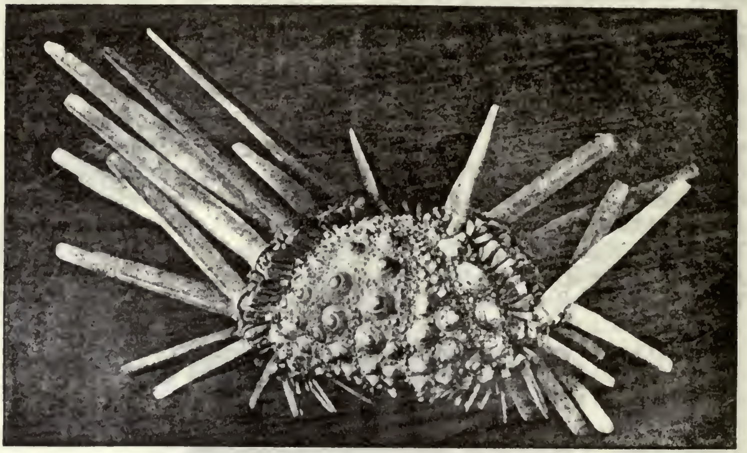


FIG. XXXIII.

Heterocentrotus mammillatus (after Agassiz), showing relation of primary and secondary spines.

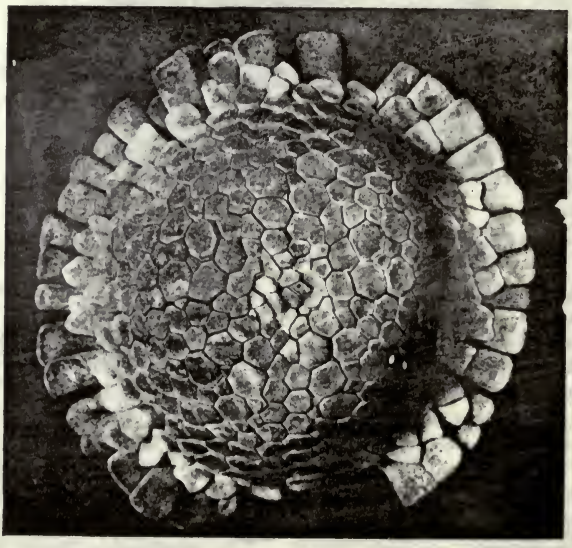


FIG. XXXIV.

Colobocentrotus atratus, showing the tessellate arrangement of the spines.

XXXIV.). The spines of the Triassic genus, *Anaulocidaris*, Zitt., had a similar arrangement.

SUB-CLASS 3. IRREGULARIA, Desor.

Echinoidea in which the anus lies outside the apical system of plates in the posterior interradius.

ORDER 1. **Gnathostomata,** Zittel.

Echinoidea Irregularia with a central peristome surrounded by a perignathic girdle; jaws present, but sometimes rudimentary. Ambulacra all similar.

This is the first of the two orders of Irregular Echinoidea, and differs from the other order—the Spatangoida—by the presence of a perignathic girdle and jaws. As in the Regular Echinoids, there is a marked tendency for the anus to pass backward out of the apical plates. In *Pygaster* the peristome is much like that of *Stomechinus*, and the ambulacral plates are sometimes compound; the jaws are fragile, but otherwise normal. The only character that excludes the genus from the Diademoida is that the anus opens outside the apical plates (Fig. XXXV. 1). *Pygaster* is thus the nearest form we know to the ancestor of all the Clypeastroid and Spatangoid sea-urchins.

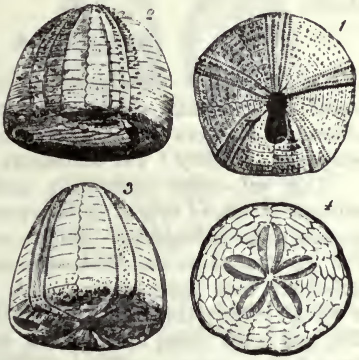


FIG. XXXV.

Irregular Echinoidea. *1, Pygaster semisulcatus*, Phil.; Jurassic. *2, Echinocorys scutatus*, Leske; Chalk. *3, Galerites albogalerus*, Leske; Chalk. *4, Scutella striatula*, Serr.; Oligocene, Malta.

The order Gnathostomata includes three main series. The first was typically Mesozoic, and was characterised by the reduction in the functional importance of the jaws, and the formation of the perignathic girdle into a high tubular peristome. From this series branches diverged in opposite directions. In one the jaws disappeared and the perignathic girdle became rudimentary; while the ambulacral plates remained as in *Pygaster*. This branch culminated in the aberrant group of the Galeritidae. Later on a second branch was given off; in this the jaws became of greater power; the ambulacra became complex, parts of them expanding into petals, the podia of which act as branchiae. The Gnathostomata may accordingly be divided into two sub-orders.

SUB-ORDER 1. HOLECTYPINA.

Gnathostomata in which the jaws are reduced in size and strength. In the most primitive members the jaws are arranged as in the Diademoida; but in later forms they are inside a tubular perignathic girdle. The jaws do not work on sockets.

This sub-order is difficult to characterise, as it includes the primitive Irregular Echinoids, as well as one series of these forms which has continued to the present day.

FAMILY 1. PYGASTERIDAE. Holectypina in which the peristome is large, and the perignathic girdle consists of disconnected processes. The ambulacra are simple and apetaloid. Genera—*Pygaster*, Ag. (Fig. XXXV. 1); *Pileus*, Desor; *Pygastrides*, Lovén; *Holectypus*, Desor; (?) *Pachyclypeus*, Desor; *Galeropygus*, Cott. FAMILY 2. DISCOIDIIDAE. Holectypina in which the peristome is small and the perignathic girdle tubular. Jaws unknown. Ambulacra apetaloid. Genera—*Discoidea*, Gray; *Protocyamus*,[1] nom. nov. FAMILY 3. GALERITIDAE. Holectypina in which the perignathic girdle is rudimentary, jaws are absent, and their place taken by ten buccal plates. Genera—*Galerites*, Lamk. (Fig. XXXV. 3); *Lanieria*, Dunc.; *Adelopneustes*, Gauth.; (?) *Coptodiscus*, Cott. & Gauth. FAMILY 4. CONOCLYPEIDAE. Holectypina in which the peristome is small; the perignathic girdle tubular and high, surrounded by five bourrelets. Genera—*Conoclypeus*, Ag.; *Oviclypeus*, Dames.

SUB-ORDER 2. CLYPEASTRINA.

Gnathostomata in which the jaws are powerful. The teeth are placed in pyramids, which articulate by a socket fitting on to vertical processes; the jaws only move horizontally, and have neither braces nor compasses (p. 289). The ambulacra are petaloid.

This sub-order includes a series of striking variations from the ordinary Echinoid type. *Echinocyamus* is the most primitive form, and appears to have developed from an ancestor closely allied to *Protocyamus*. The great advance in *Echinocyamus* is the expansion of parts of the ambulacra into rudimentary petals (Fig. XXXVI.); in the upper part of the ambulacra the outer pores of the pore-pairs have increased to small slits, and occur along curved lines, enclosing somewhat leaf-shaped areas. Beyond these only a single pore occurs in each ambulacral plate. The perignathic girdle of *Echinocyamus* consists of five vertical pegs, rising from the interradial peristomial plates; this reminds us of *Galerites*, in which the perignathic girdle is reduced to five interradial thickenings. The structural differences between *Protocyamus* and *Echinocyamus* are small, and their importance is exaggerated by the different shape of the tests. But *Echinocyamus* was succeeded by a very divergent series. Most of the members of the group are long, broad, and low; some are thin and flat. In these cases the upper surface regains the support it loses owing to departure from the dome-shaped form, by the development of pillars which pass from floor to roof. The ambulacra in the typical forms are petaloid, and the podia in these areas expand to act as branchiae (Fig. XXXVI.). In some cases pores only occur in the petals; in others they are scattered over the test, occurring on both radial and interradial plates. In some genera, such as *Laganum*, though the petaloid portions of the ambulacra are broad, they are narrower than the ambulacral plates in the extra-petaloid portions which expand laterally, and are much broader than the interambulacra. In the simplest members of this group the interambulacra are, however, "continuous" from apical system to peristome (as in *Laganum*); but in the more advanced, such as *Rotula*, the interambulacra are "discontinuous," the ambulacra meeting one another and cutting off the interambulacral peristomial plate from its connection with the rest of the interambulacrum. Another feature peculiar to this sub-order is the presence of a series of furrows on the lower surface of the test; these are known as the actinal furrows, and they are either straight, as in the Clypeastridae, or bifurcating, as in the Scutellidae.

---

[1] A name suggested in lieu of *Echinites* proposed by Duncan, but preoccupied by Leske for Echinoids, and by Müller and Troschel for Asteroidea; the name is selected to indicate the affinity of this echinoid with the *Echinocyamus* series.

Family 1. Fibulariidae. Clypeastrina with ambulacra in rudimentary open petals. The interambulacral plates are continuous. The pillars are slightly developed. The perignathic girdle consists of five single interradial processes. The peristomial interradial plate is large. Genera—*Echinocyamus*, Phelsum (Fig. XXXVII.); *Scutellina*, Ag.; *Sismondia*, Desor; *Fibularia*, Lam.; *Thegaster*, Pomel.

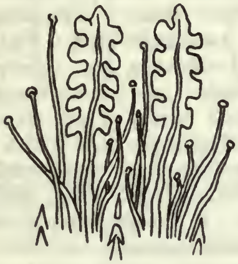


Fig. XXXVI.

Branchial podia from petaloid portion of ambulacrum of *Clypeaster*.

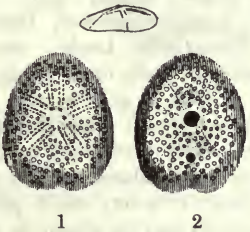


Fig. XXXVII.

Echinocyamus pusillus. 1, upper surface showing simple petals and four genital pores; 2, the lower surface showing the anus intermediate between the central mouth and the posterior border.

Family 2. Laganidae. Clypeastrina with ambulacra petaloid; numerous pores for prehensile podia occur in addition to the large pores for the respiratory podia. The interambulacral plates are "continuous"; the peristomial plate is medium in size and bears a single perignathic process. The actinal furrows are simple and straight. Genus—*Laganum*, Blainv.

Family 3. Scutellidae. Flat Clypeastrina with closed petaloid ambulacra. The interambulacral plates are "discontinuous" in some or all of the areas; the peristomial plate is large and bears a single perignathic process. The actinal furrows are bifurcating. Genera—*Scutella*, Lam. (Fig. XXXV. 4); *Echinarachnius*, Leske; *Echinodiscus*, Ag.; *Encope*, Ag.; *Monophora*, Ag.; *Mellita*, Ag.; *Melitella*, Dunc.; *Astriclypeus*, Verrill; *Lenita*, Desor; *Mortonia*, Desor; *Rotula*, Ag. (Fig. IX.); *Rotuloidea*, Etheridge; *Moulinsia*, Ag.; (?) *Runa*, Ag. The most striking feature in this family is the extreme thinness and flatness of the tests. In some species, such as *Scutella striatula*, the test may be 100 mm. in diameter, and only 10 mm. in height. The upper surface accordingly needs greater support than it could obtain from the margin of the test; this is given by numerous pillars which connect the upper and lower walls. The external margin is often notched, as in *Scutella*; the notches may deepen into "slits" separated by finger-shaped processes, as in *Rotula* (Fig. IX.). In some genera two adjacent processes unite at their free ends, and a hole is left through the test; such holes are known as "lunules," and occur in *Mellita*, *Monophora*, etc. All the interambulacral areas are discontinuous in some genera, *e.g. Encope*, but in *Rotula* and *Mellita* one or two of the areas may be continuous from peristome to apex.

FAMILY 4. CLYPEASTRIDAE. Clypeastrina with closed petaloid ambulacra. The interambulacral plates are discontinuous; the peristomial plate is small. There are two perignathic processes in each area, and they are ambulacral in position. The actinal furrows are straight. SUB-FAMILY 1. CLYPEASTRINAE. Massive Clypeastridae with closed petals; usually high. Genera—*Clypeaster*, Lam.; *Echinanthus*, Leske (= *Diplothecanthus*, Dunc.); *Plesianthus*, Dunc.; *Anomalanthus*, Bell; *Monostychia*, Laube. SUB-FAMILY 2. ARACHNOIDINAE. Flat, low Clypeastridae with open petals. Genera—*Arachnoides*, Ag.; *Alexandria*, Pfeffer. These genera are usually included as a sub-family of Scutellidae, which they resemble in external form. Their structure, however, allies them more nearly with the Clypeasters, with which they agree in all fundamental characters. They differ from the Scutellidae by having (1) a very small peristomial interambulacral plate, which in some species may be absent in several areas; (2) straight, simple, actinal furrows; (3) five pairs of ambulacral perignathic processes.

ORDER 2. **Atelostomata**, Zittel.

Echinoidea Irregularia, in which there are no jaws, teeth, perignathic girdle, or external branchiae.

The Atelostomata introduce three additional structures, upon which the classification within the order depends. These are the sternum, floscelle, and fasciole. In Echinoids previously considered the mouth is central or sub-central, and the five areas around it are of equal importance; but as the mouth becomes eccentric in position, one interradius necessarily becomes longer than the rest. The anus is situated in this interradius, which requires some modification of the plates for the sake of increased strength. In the simplest of the Atelostomata the plates of the posterior interradius are but slightly different from those of the other areas but the plates are larger, and dovetail more deeply into one another. In *Collyrites* there is a slight advance on this plan, and in genera such as *Echinocorys* and *Holaster* the plates dovetail so deeply as to form a strong sternum along the under side of the test. This type is known as the "meridosternous" (Fig. XXXVIII. 1). In the next stage the first pair of plates in the interambulacrum increase in length, and both are in contact with the peristomial plate of the same area, as in *Toxaster* (Fig. XXXVIII. 2). This is the "amphisternous" type, the extreme form of which we see in *Spatangus purpureus* (Fig. XXXVIII. 4).

We have seen that the upper parts of the ambulacra of *Clypeaster*, etc., are modified into petals. In one section of the Atelostomata there is an analogous expansion of the ambulacra round the peristome into "floscelles."

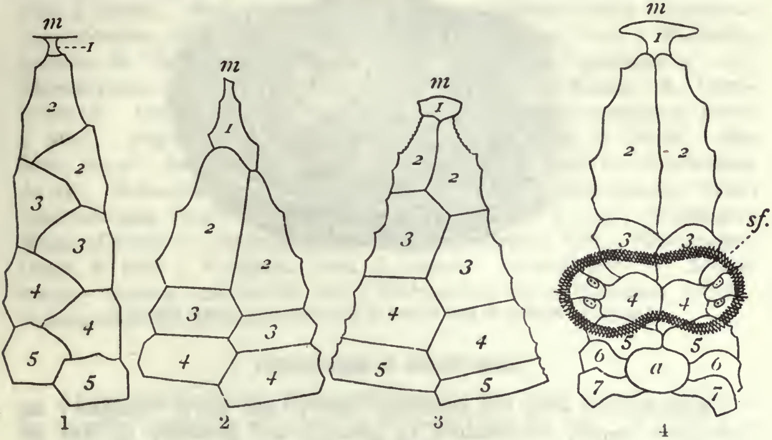


FIG. XXXVIII.

The types of Spatangoid Sterna. 1, meridosternous; 3, 4, amphisternous; 2, intermediate. 1, *Echinocorys scutatus*; 2, *Toxaster ricordeanus*; 3, *Cassidulus pacificus*; 4, *Spatangus purpureus*. *m*, mouth; *a*, anus.

The peristomial interambulacral plates are raised into projecting ridges known as "bourrelets"; while the ambulacra are expanded into leaf-shaped areas known as "phyllodes." The pore-pairs of the phyllodes are much larger than those of the rest of the ambulacrum. The five bourrelets and five phyllodes together form the floscelle, which is typical of the Cassidulidae.

Among the Atelostomata large spines like those of *Cidaris* are never found. The spines are very numerous and generally small, forming a fur over the test. In some cases specially modified spines occur crowded together along bands (Figs. XXXIX.-XLI.), forming "fascioles." There are five different varieties: (1) The "peripetalous," which encloses the petaloid portions of the ambulacra; (2) the "subanal" (*sf* in Fig. XXXVIII. 4), which encloses a space, or "plastron," below the anus; (3) the "marginal," along the border of the test; (4) the "internal," which crosses the petaloid portions of the ambulacra; and (5) the two "lateral," which run from the peripetalous to below the anus. All five kinds of fascioles never occur together in the same Echinoid.

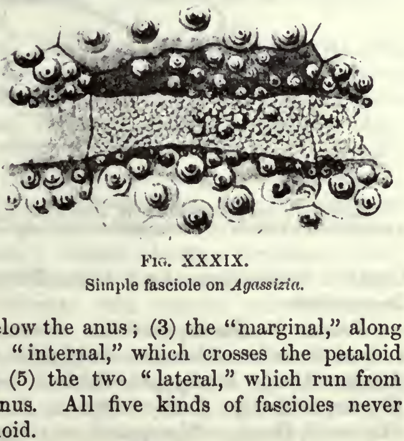


FIG. XXXIX.

Simple fasciole on *Agassizia*.

The Atelostomata include two main divisions, which develop along somewhat parallel lines.

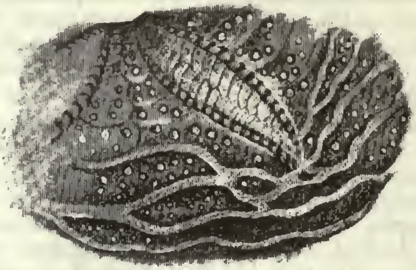


FIG. XL.

Compound fasciole on part of test of *Macropneustes*. (After Agassiz.)

SUB-ORDER 1. ASTERNATA.

Atelostomata with the peristome central and never bilabiate ; the ambulacra simple, sub-petaloid, or petaloid, and generally all five are similar. Floscelle generally present. No sternum.

FAMILY 1. ECHINONËIDAE. Asternata with narrow, apetaloid, similar ambulacra, and without floscelle. Genera—*Echinonëus*, Van Phelsum ; *Galeroclypeus*, Cott. ; *Galeropygus*, Cott. ; *Hyboclypeus*, Ag. ; *Infraclypeus*, Gauth. ; *Nucleopygus*, Ag. ; *Pileus*, Desor ; *Pachyclypeus*, Desor ; *Pyrina*, Desmoulins.

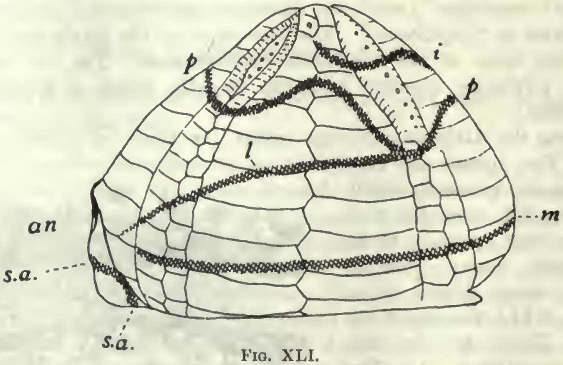


FIG. XLI.

Diagram of a Spatangoid Echinoid, showing arrangement of the fascioles. *i*, internal fasciole ; *a*, peripetalous fasciole ; *l*, lateral fasciole ; *m*, marginal fasciole ; *s.a*, subanal fasciole ; *a.n*, anus.

FAMILY 2. NUCLEOLITIDAE. Asternata with sub-petaloid ambulacra and no floscelle. Genera—*Amblypygus*, Ag. ; *Anochanus*, Grube ; *Anorthopygus*, Cott. ; *Botriopygus*, d'Orb. ; *Caratomus*, Ag. ; (?) *Desorella*, Cott. ; *Haimea*, Michelin ; *Ilariona*, Dames ; *Nucleolites*, Lam. (syn. *Echinobrissus*) ; *Oligopodia*, Dunc. ; *Oligopygus*, Lor. ; *Pygaulus*, Ag. ; *Trematopygus*, d'Orb.

Family 3. Cassidulidae. Asternata with closed, petaloid ambulacra a floscelle is present. Sub-Family 1. Clypeina. Genera—*Clypeus*, Leske; *Clypeopygus* and *Faujasia*, d'Orb.; *Pseudodesorella*, Étallon; *Pygurostoma*, Cott. & Gauth.; *Pygurus*, Ag. Sub-Family 2. Cassidulinae. Genera—*Australanthus*, Bittner; *Breynella*, Greg.; *Cassidulus*, Lam.; *Eurhodia*, Archiac & Haime; *Paralampas*, Dunc. & Slad.; *Pygorhynchus*, Ag.; *Rhynchopygus*, d'Orb.; *Stigmatopygus*, d'Orb. Sub-Family 3. Catopyginae. Genera—*Catopygus*, Ag. (Fig. XVI. 8); *Neocatopygus*, Dunc. & Slad.; *Phyllobrissus*, Cott.; *Pseudocatopygus*, Cott. & Gauth.; *Studeria*, Dunc. Sub-Family 4. Echinolampinae. Genera—*Conolampas*, A. Ag.; *Echinolampas*, Gray; *Heteroclypeus*, Cott.; *Microlampas*, Cott.; *Craterolampas*, Cott.; *Milletia*, Dunc.; *Neolampas*, A. Ag.; *Oriolampas*, Munier-Chalmas; *Palaeolampas*, Bell; *Phylloclypeus*, Lor.; *Plesiolampas*, Dunc. & Slad.; *Vologesia*, Cott. & Gauth. Sub-Family 5. Eolampinae. Genera—*Archiacia*, Ag.; *Asterostoma*, Ag.; *Claviaster*, d'Orb.; *Eolampas*, Dunc. & Slad.

Sub-Order 2. Sternata.

Atelostomata with the peristome eccentric anteriorly (usually bilabiate). No floscelle; anterior ambulacrum different from the rest. A sternum is present. Fascioles sometimes present.

Family 1. Collyritidae. Sternata without floscelle. There is a rudimentary meridosternum. The anterior ambulacrum is narrower than the others. Apical system disjunct; the three anterior ambulacra grouped together as the "trivium," and the two postero-lateral ambulacra as the "bivium." There are no fascioles. Genera—*Collyrites*, Desmoulins; *Dysaster*, Ag. (Fig. XVI. 6); *Grasia* and (?) *Metaporhinus*, Michelin; *Pygorhytis*, Pomel. Owing to the disjunct apical system, this family has completely lost the radial symmetry, and presents some remarkable resemblances to the Pourtalesiidae. It appears, however, probable that while the Collyritidae have descended from some primitive asternate form allied to *Hyboclypus*, the Pourtalesiidae are degenerate forms of Prymnodesmian Sternata.

Family 2. Echinocorythidae. Meridosternous, labiate Sternata, with an elongate apical system, and the ambulacra separated into a bivium and trivium. Fascioles present in some genera. Genera—*Calymne*, Wyv. Thoms.; *Cardiaster*, Forbes; *Coraster*, Cott.; *Cystechinus*, A. Ag.; *Echinocorys*, Leske (syn. *Ananchytes*, Lam., Fig. XXXV. 2); *Enallopneustes*, Pomel; *Enichaster*, Lor.; *Entomaster*, Gauth.; *Galeaster*, Seunes; *Guettaria*, Gauth.; *Hagenovia*, Dunc.; *Hemipneustes*, Ag.; *Holaster*, Ag. (sub-gen. *Sternotaxis*, Lamb.); *Infulaster*, Hagenow; *Jeronia*, Seunes; *Lampadaster*, Cott.; *Offaster*, Desor; *Oolaster*, Laube; *Ovulaster*, Cott.; *Stegaster*, Pomel; *Stenonia*, Desor; *Tholaster*, Seunes; *Urechinus*, A. Ag.

Family 3. Spatangidae. Sternata with anterior ambulacrum reduced; apical system compact; sternum either amphisternous or meridosternous. Section 1. Adetinae. Spatangidae without fascioles. Genera—*Archaeopneustes*, Greg.; *Clypeanthus*, Cott.; *Echinocrepis*, A. Ag.; *Enallaster*, d'Orb. (Fig. XVI. 7); *Epiaster*, d'Orb.; *Genicopatagus*, A. Ag.; *Hemipatagus*, Desor; *Heterolampas*, Cott.; *Isaster*, Desor; *Macraster*, Roem.; (?) *Megalaster*, Dunc. ; *Palaeobrissus*, A. Ag. ; *Palaeopneustes*, A. Ag. ; *Platybrissus*, Grube ; *Spatagocystis*, A. Ag. ; *Toxaster*, Ag. SECTION 2. PRYMNADETINAE. Spatangidae with fascioles, but no subanal fasciole. Genera—*Abatus*, Desor ; *Aceste* and *Aerope*, Wyv. Thoms. ; *Agassizia*, Valentin ; *Brissopsis*, Ag. (Fig. XLII.) ; *Coraster*, Cott. ; *Dipneustes*, Cott. ; *Faorina*, Gray ; *Hemi-*

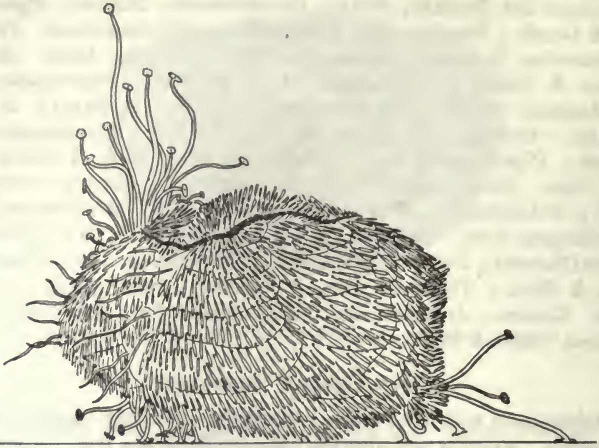


FIG. XLII.

Brissopsis lyrifera, Forbes, sp., showing podia in action, and peripetalous fasciole. (After Lovén).

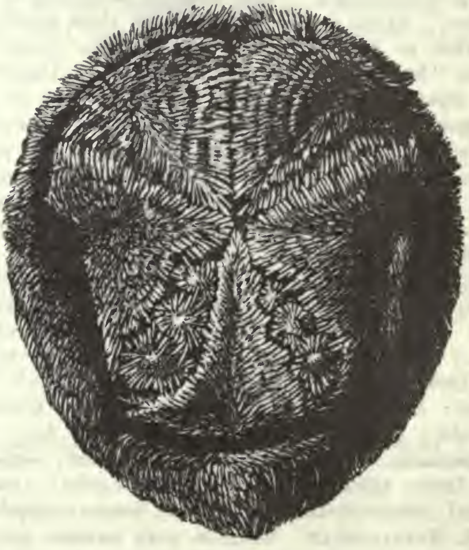


FIG. XLIII.

Hemiaster Philippii, with young echinoids in the marsupia. (After Wyville Thomson.)

aster, Desor (Fig. XLIII.); *Homoeaster* and *Hypsospatagus*, Pomel; *Iraniaster*, Cott. & Gauth.; *Lambertiaster*, Gauth.; *Linthia*, Merian; *Moira*, A. Ag.; *Moiropsis*, A. Ag.; *Ornithaster*, Cott.; *Pericosmus*, Ag.; *Prenaster*, Desor; *Schizaster*, Ag. SECTION 3. PRYMNODESMINAE. Spatangidae with subanal fasciole. Genera — *Argopatagus*, A. Ag.; *Brissopatagus*, Cott.; *Brissus*, Leske; *Breynia*, Desor; *Cionobrissus*, A. Ag.; *Cleistechinus*, Lor.; *Cyclaster*, Cott.; *Echinocardium*, Gray; *Eupatagus*, Ag.; *Gaultieria*, Desor; *Gibbaster*, Gauth.; *Homolampas*, A. Ag.; *Isopneustes*, Pomel; *Linopneustes*, A. Ag.; *Lovenia*, Ag. & Desor; *Linchophorus*, Dames; *Macropneustes*, Ag.; *Maretia*, *Meoma*, and *Metalia*, Gray; *Micraster*, Ag.; *Nacospatangus*, A. Ag.; *Neopneustes*, Dunc.; *Palaeotropus*, Lovén; *Pygospatangus*, Cott.; *Rhinobrissus*, A. Ag.; *Sarsella*, Pomel; *Spatangomorpha*, Böhm; *Spatangus*, Leske (Figs. XLIV., XLV.); *Stomoporus*, Cott.; *Tuberaster*, Peron & Gauthier.

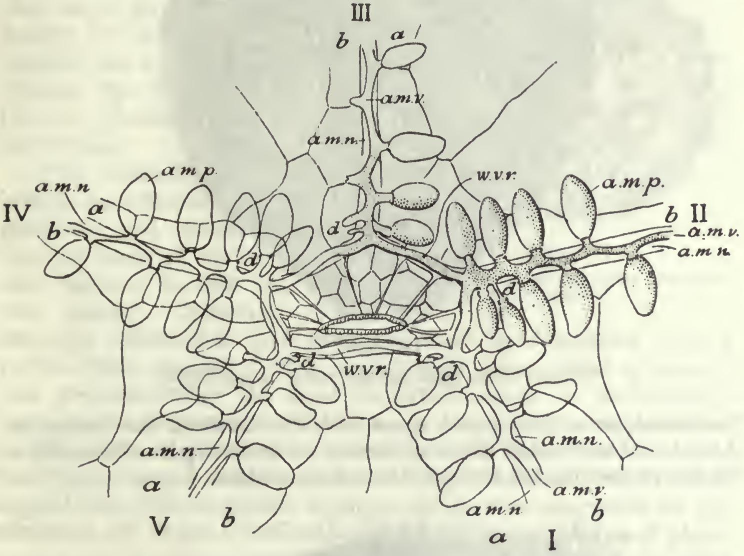


FIG. XLIV.

Peristomial region of *Spatangus purpureus* seen from inside the test (after Lovén). I-V, the five ambulacra in which the vertical series are each marked *a* or *b*.

FAMILY 4. PALAEOSTOMIDAE. Sternata with a pentagonal, alabiate peristome, provided with five buccal plates; a peripetalous fasciole. Genus—*Palaeostoma*, Lovén (*Leskia*, Gray).

FAMILY 5. POURTALESIIDAE. Sternata with apetalous, flush ambulacra. Peristome in a deep anterior recess. Form elongate; flat or oral surface. The ambulacral plates are uniporous (Fig. XLVI.). This family includes perhaps the three most perplexing of recent Echinoids; but owing to the extreme fragility of the tests their study is difficult, and owing to their great variability the classification is at present unsatisfactory. The typical genus *Pourtalesia* is the subject of an elaborate memoir by Lovén (58). It has a disconnected apical system, the postero-lateral interambulacra meeting across it. In this and some other respects it resembles *Collyrites;* but it has a sub-anal fasciole, and is probably to be regarded as a degenerate Spatangid rather than a direct descendant of the Mesozoic Collyritidae.

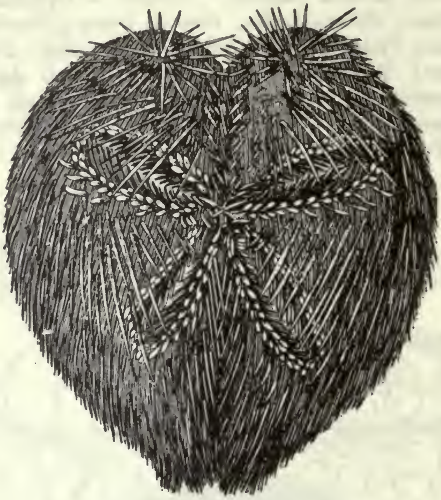


Fig XLV.

The Heart Urchin (*Spatangus purpureus*). Abactinal side.

The second genus *Spatagocystis* agrees with *Pourtalesia* in the disruption of the apical system, but it has no fasciole. The third genus *Echinocrepis* also has no fasciole, but the apical system is compact.

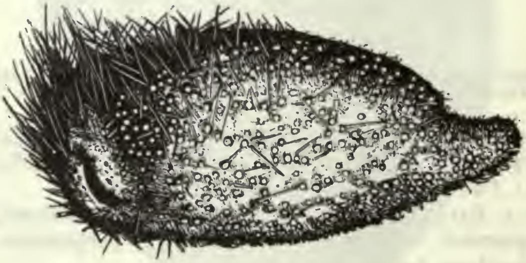


Fig. XLVI.

Pourtalesia Jeffreysi (Wyv. Thomson).

We are now in a position to discuss briefly, first, the relations of the Echinoidea to the other classes of Echinoderma, and secondly, the lines of evolution within the class itself. (Compare Chapter VIII. pp. 17, 33.)

Each of the main groups of Echinoderma has been at one time regarded as the ancestor or nearest ally of the Echinoids, and the question is still highly conjectural. Embryology gives very little assistance. Study of the development of a young Echinothurid, *Echinocyamus*, or *Hemiaster* (Fig. XLVII.) teaches important lessons as to the affinities between those forms and other Echinoids. It shows that the young Echinothurid resembles the Diademoida, and that the young *Hemiaster* is endocyclic. But the earlier larval stages have been so affected by secondary variations that they give no satisfactory information as to whether the Echinoids are nearest to the Cystids, Crinoids, Holothurians, or Stelleroids.

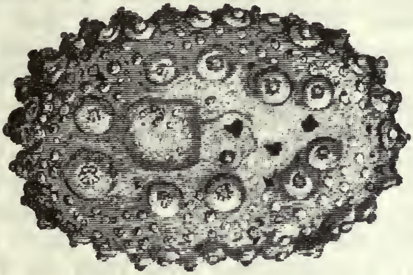


Fig. XLVII.

Larval form of *Hemiaster cavernosa*, in the endocyclic stage. (After Agassiz.)

The Crinoids are so unlike the Echinoids in appearance and structure, that we know of no form that appears to link the two classes. Nevertheless, the Echinoidea have been regarded as descended from a Crinoid-like ancestor. The acquirement of a radial symmetry was unquestionably the most important event in the development of the ancestral Echinoderm; it is easiest to explain this as the result of fixation, and therefore the fixed, stalked forms have been claimed as the ancestors of the free forms. It is further argued that this conclusion is supported by the occurrence on the abactinal side of some Echinoids and Stelleroids of a series of plates known as the apical system. This system includes a central plate surrounded by two circles of plates. The theory has been urged, especially by the late P. H. Carpenter and by W. P. Sladen, that the plates of this apical system are homologous with those of the calyx of the Pelmatozoa, and are to be regarded as relics from a period when these plates were of great functional importance. Unfortunately for this view, however, the calycinal or apical plates are either absent or unimportant in the oldest Echinoids and Asteroids; and it is in later groups, such as the Saleniidae and Cidaridae, that the plates are developed on the supposed ancestral plan. Moreover, instead of *Tiarechinus*—in which the apical plates are most important—being ancestral, it is almost certainly an aberrant, and somewhat degenerate offshoot.

The last blow to the idea of the apical plates of Echinoids being homologous with the calyx plates of Crinoids, has been given by MacBride, who, on embryological grounds, urges that the abactinal poles of Asteroids and Crinoids, on which these plates develop, have nothing to do with one another. MacBride recognises the influence of fixation on the anatomy of Starfish and Echinoids, but maintains that such fixation was by the actinal surface in these two classes, whereas in Crinoids it was by the abactinal surface. (See, however, Chapter VIII. p. 14.)

The question as to which of the groups of organs first acquired the radial character is of great importance in connection with the origin of the Echinoderma. The Sarasins, who made a detailed study of the Echinothuridae, were much impressed with the importance of the radial muscles, and suggested that it was the muscles that first became pentamerous. There are many striking points of resemblance between such a form as *Asthenosoma* and the Holothurians. The Sarasins therefore ridiculed the supposed Crinoid ancestor as a "Crinoid phantom," and derived the Echinoidea from the Holothurians. This argument is based on the idea that the primitive characters of the Echinothuridae are due to inheritance from the ancestral Echinoid. But it appears most probable that the Echinothuridae arose from the Diademoid *Pedina*, or from some close ally of that genus. The primitive characters of the Echinothuridae are therefore secondarily acquired, and are not original. The immediate ancestor of the family lived in the Jurassic, and not in the Palaeozoic seas. To accept this conclusion means to abandon the derivation of the Echinoids from the Holothurians.

Leuckart, in 1848, separated the Echinoderma into the three groups of the Pelmatozoa, Echinozoa, and Scytodermata, and this classification is still generally used in practice. In the two latest arrangements of the Echinoderma, those of Bell and Haeckel, the Echinoids are still grouped with the Stelleroids. They undoubtedly agree in several important characters, the members of both classes having the gonads pentamerous, the oral surface kept downward, and power of locomotion.

The class Stelleroidea is older than that of the Echinoidea, but we know of no member of the former that can be regarded as the ancestor of the latter.

The evidence in favour of the origin of Echinoids from Cystids or allied forms is more weighty. Neumayr advocated this view (64, 65), and it has recently received fresh support from Haeckel (36 on p. 213). Neumayr included *Echinocystis* in the Cystidea. The genus is, however, here included among the Echinoids. The uncertainty as to its position shows that there is an approximation between the two classes. We are, therefore, forced to the position that one group[1] of primitive Pelmatozoa diverged from the main stem and approximated to the Echinoids; and that it was succeeded by Echinoids so similar in structure that it is hard to draw a satisfactory line of separation.

---

[1] Separated in Chapter XII. as a Class—Edrioasteroidea.

Although the ancestral Echinoid is still unknown, the main lines of evolution in the class are clearly recognisable. The Echinoids began with forms having small, sac-like bodies, and a mouth and anus at opposite poles; the body was muscular, supported by a series of angular plates, of which five pairs were perforated by pores. At the summit of the test occurred the apertures of the alimentary, generative, and water-vascular systems; and the apertures of these systems were supported and held in place by a series of special plates.

At first the palaeontological record is incomplete, the plates of the test being thin, fragile, and loosely fitted together. Hence there is a gap between the Echinoid just described and its next known successors, in which the interradial plates are irregular, and the apical system of plates is absent. But as the skeleton thickens, fossils become more abundant and better preserved. We can see the increase in the number of interambulacral and of ambulacral plates up to forms such as *Melonites.* Then, as the plates became stouter, the flexibility of the test was lost; thus the advantage of having small, numerous plates was lost. Hence the Echinoids with more than twenty rows of plates disappeared, and were succeeded by a group, the main feature of which was the consolidation of the test. About the same time there appeared an offshoot from the main stem, in which the test was strengthened by a great development of the apical system; this arrangement reached its highest development in two aberrant genera (*Tiarechinus* and *Lysechinus*) which lived in the Triassic coral lagoons of the Tyrol. The Melonitoida and Plesiocidaroida apparently left no issue, and all existing and post-Triassic Echinoids appear to have descended from the primitive genera of Cidaroida.

From *Cidaris,* with its ambulacra of simple primary plates, the more complex types were developed by the crowding of the pore-pairs, and the decrease in size and increase in number of the spines; hence the ambulacral plates become compound, and the interambulacral plates bore numerous tubercles and granules, and thus gave rise to the various groups of Regular Echinoidea. In some deep-sea forms the calcification of the external skeleton is imperfect; the plates are thin and the muscles strong; by the imbrication and isolation of the plates there is a return to some of the features of the flexible Palaeozoic Echinoids.

The main departure from the type of regular Echinoids is due to the backward movement of the anus interfering with the originally quinqueradiate arrangement of the organs (Fig. XLVI.). The mouth passes forward, the jaws disappear, the ambulacral podia become specialised for respiration as well as locomotion, the apical system of plates becomes compact, elongate, disjunct, or rudimentary, and a bilateral symmetry replaces the primitive, pentameral symmetry. At first the jaws are retained; but as the body becomes bilateral, the mouth is constricted, and room for play of the jaws is lessened. No doubt all Echinoids get a proportion of nourishment from the mud and sand which they swallow; but as their jaws become smaller, and they can browse less effectively, the importance of this food-supply becomes more important. The development of a projecting under lip below the mouth was an advantage to the Echinoid, by enabling it to swallow more food. Hence the Irregular Echinoids began with teeth and a central mouth—a type first met with in the lower Jurassic; later on, in the Jurassic, came the second type, in which there are no jaws and the mouth is eccentric; the former is the order Gnathostomata, and the latter the order Atelostomata. The Gnathostomata began in the Jurassic with the genus *Pygaster*, which differs from the regular ectobranchiate Echinoids only by the anus opening behind the apical system; the Pygastridae were succeeded in the Cretaceous by the Discoidiidae, from one genus of which, *Protocyamus*, there is an easy passage to the Fibulariidae, and thus to the sub-order Clypeastrina.

The order Atelostomata has apparently also been derived from a genus allied to *Pygaster*. The jaws are lost, and the apical system either remains compact or becomes elongate: the former series possibly began with *Galeropygus*, whence the rest of the asternate forms were derived. The series with elongate apical systems began with some such genus as *Hyboclypeus*, which led the way to the Collyritidae and Echinocorythidae, whence the higher Spatangid Echinoids descended.

LITERATURE OF ECHINOIDEA.

1. *Agassiz, A.* 1872-74. (Revision of the Echini.) Ill. Cat. Mus. Comp. Zool. Harvard, No. vii. 2 vols. 762 pp. 94 pls.
2. —— 1881. (Report on the Echinoidea dredged by H.M.S. *Challenger* during the years 1873-76.) Rep. Chall. Exped. Zool., vol. iii. 321 pp. 45 pls.
3. —— 1883. (Report on the Echini. Results of dredging by the *Blake*, No. xxiv. pt. 1.) Mem. Mus. Comp. Zool. Harvard, vol. x. No. i. 94 pp. 32 pls.
4. *Agassiz, L.* 1835. (Prodrome d'une Monographie des Radiaires ou Échinodermes.) Mém. Soc. Sci. Nat. Neuchâtel, vol. i. pp. 168-199.
5. *Agassiz, L., Desor, E., and Valentin, G.* 1838-42. Monographies d'Échinodermes vivans et fossiles, Nos. i.-iv.; and Anatomie, No. i. 4to, Neuchâtel.
6. *Agassiz, L., and Desor, E.* 1846-48. (Catalogue raisonné des familles, des genres et des espèces de la classe des Échinodermes.) Ann. Sci. Nat. Zool., ser. 3, vols. vi., vii., and viii. 167 pp. 2 pls.

7. *Bell, F. J.* 1881. (The Echinometridae.) Proc. Zool. Soc. for 1881, pp. 410-433.
8. —— 1889. (Report of a Deep-sea Trawling Cruise off the S.W. Coast of Ireland. Echinodermata.) Ann. Mag. Nat. Hist., ser. 6, vol. iv. pp. 432-445, pls. xviii., xix.
9. —— 1891. (On the Arrangement and Inter-relations of the Classes of the Echinodermata.) Ann. Mag. Nat. Hist., ser. 6, vol. viii. pp. 206-215.
10. —— 1892. Catalogue of the British Echinoderms in the British Museum, xvii. and 202 pp. 16 pls.
11. *Bütschli, O.* 1892. (Versuch des Ableitung des Echinoderms aus einer bilateralen Urform.) Zeitschr. Wiss. Zool., vol. liii. Suppl. pp. 136-160, pl. ix.
12. *Clark, W. B.* 1893. (The Mesozoic Echinodermata of the United States.) Bull. U.S. Geol. Surv. No. 97, 207 pp. 50 pls.
13. *Cotteau, G. H.* 1862-67. (Échinides réguliers.) Paléontologie française, Terrains crétacées, vol. vii. 894 pp. 198 pls.
14. —— 1867-85. (Échinides irréguliers et réguliers.) Paléont. française, Terrains jurassiques, vol. ix. 1867-74, 552 pp. 142 pls. ; vol. x. pt. i. 1875-80, 468 pp. 120 pls. ; vol. x. pt. ii. 1880-85, 960 pp. 258 pls.
15. —— 1885-94. (Échinides.) Paléont. française, Terrains tertiaires (Éocène), vol. i. 1885-89, 672 pp. 200 pls. ; vol. ii. 1889-94, 788 pp. 176 pls.
16. *Cotteau, G. H., Peron, P. A., and Gauthier, V.* 1876-91. Échinides fossiles de l'Algérie, 3 vols. 8vo, Paris.
17. *Cotteau, G. H., and Triger.* 1857. Échinides du département de la Sarthe. 8vo, Paris, 458 pp. 75 pls.
18. *Desmoulins, C.* 1835-37. Mémoires sur les Échinides. 8vo, Bordeaux, 520 pp. 2 pls.
19. *Desor, E.* 1855, 1857-58. Synopsis dès Échinides fossiles. 4to, Genève, Paris, and Wiesbaden, lxiv. and 490 pp. 43 pls.
20. *Döderlein, L.* 1887. Die Japanesischen Seeigel, Theil 1. 4to, Stuttgart, 59 pp. 11 pls.
21. *Dujardin F., and Hupé, H.* 1862. Histoire naturelle des Zoophytes Échinodermes. 8vo, Paris, 628 pp. 10 pls.
22. *Duncan, P. M.* 1885. (Structure of the Ambulacra of some Fossil Genera and Species of Regular Echinoidea.) Quart. Journ. Geol. Soc., vol. xli. 1885, pp. 419-453.
23. —— 1888. (On some Points in the Anatomy of the Temnopleuridae.) Ann. Mag. Nat. Hist., ser. 6, vol. i. pp. 109-131, pl. xi.
24. —— 1890. (A Revision of the Genera and Great Groups of the Echinoidea.) Journ. Linn. Soc. Zool., vol. xxiii. pp. 1-311.
25. *Duncan, P. M., and Sladen, W. P.* 1882-86. (The Fossil Echinoidea of Sind.) Pal. Ind., ser. xiv. vol. i. pt. 3, 382 pp. 58 pls.
26. —— —— 1883. (The Fossil Echinoidea of Kachh and Kattywar.) Pal. Ind., ser. xiv. vol. i. pt. 4, 104 pp. 13 pls.
27. *Gauthier, V.* 1889. (Description des Échinides fossiles recueillis . . . dans la région sud des hauts-plateaux de la Tunisie, par M. P. Thomas.) Exploration Scient. Tunisie. Paris, 116 pp. in 8vo, 6 pls. in 4to.
28. —— 1892. Notes sur les Échinides crétacés recueillis en Tunisie, par M. Aubert. 8vo, Paris, annexe de la carte géol. de la Tunisie, 52 pp. 4 pls.
29. *Gray, J. E.* 1825. (An Attempt to Divide the Echinida or Sea-Eggs into Natural Families.) Ann. Phil., vol. x. pp. 423-431.

30. *Gray, J. E.* 1855. Catalogue of the Recent Echinida or Sea-Eggs in the Collection of the British Museum. 8vo, London, 69 pp. 6 pls.
31. *Gregory, J. W.* 1891. (The Maltese Fossil Echinoidea.) Trans. Roy. Soc. Edinb., vol. xxxvi. pt. 3, pp. 585-639, 2 pls.
32. —— 1891. (The Relations of the American and European Echinoid Faunas.) Bull. Geol. Soc. Amer., vol. iii. pp. 101-108.
33. —— 1891. (A Revision of the British Fossil Cainozoic Echinoidea.) Proc. Geol. Assoc., vol. xii. pp. 16-60, pls. i., ii.
34. —— 1897. (On *Lysechinus*, a new Genus of Fossil Echinoderms from the Tyrolese Trias.) Proc. Zool. Soc. for 1896, pp. 1000-1005, pl. li.
35. —— 1897. (On the Affinities of the Echinothuridae.) Quart. Journ. Geol. Soc., vol. liii. pp. 112-122, pl. vii.
36. —— 1897. (On *Echinocystis* and *Palaeodiscus*—two Silurian genera of Echinoidea.) *Tom. cit.* pp. 123-136, pl. vii.
37. *Groom, T. T.* 1887. (On some new Features in *Pelanechinus corallinus.*) Quart. Journ. Geol. Soc., vol. xliii. pp. 703-714, pl. xxviii.
38. *Hamann, O.* 1887. (Beitrage zur Histologie der Echinodermen, Heft 3. Anatomie und Histologie der Echiniden und Spatangiden.) Jena. Zeitschr., vol. xxi. pp. 87-266, pls. vi.-xviii.
39. *Hartog, M. M.* 1887. (The True Nature of the "Madreporic System" of Echinodermata.) Ann. Mag. Nat. Hist. (5), vol. x. pp. 321-326.
40. *Hoffmann, C. K.* 1871. (Zur Anatomie der Echinen und Spatangen.) Niederl. Arch. Zool., vol. i. pp. 11-112, pls. iii.-x.
41. *Jackson, R. T.* 1896. (Studies of Palæechinoidea.) Bull. Geol. Soc. Amer., vol. vii. pp. 171-254, pls. ii.-ix.
42. *Jaekel, O.* 1894. (Ueber Bothriocidaris.) Sitz. Ges. naturf. Berlin für 1894, pp. 243-255.
43. *Köhler, R.* 1883. (Recherches sur les Échinides des côtes de Provence.) Ann. Mus. Hist. Nat. Marseilles, vol. i. 167 pp. 6 pls.
44. *Lambert, J.* 1889. (Note sur le développement de *l'Échinospatangus neocomiensis.*) Bull. Soc. Sci. Yonne, vol. xliii. 19 pp.
45. —— 1892. (Recherches sur les Échinides de l'Aptien de Grandpré.) Bull. Soc. Géol. France, ser. 3, vol. xx. pp. 38-100, pls. ii.-iv.
46. —— 1893. (Études morphologiques sur le Plastron des Spatangides.) Bull. Soc. Sci. Yonne, vol. xlvi. section ii. pp. 55-98 and folding table.
47. *Lang, A.* 1894. Lehrbuch der vergleichenden Anatomie, Vierte Abtheilung. 8vo, Jena. Translated by H. M. and M. Bernard, as Text-book of Comparative Anatomy, pt. ii. 1896, London.
48. *Leske, N. G.* 1778. Additamenta ad Jacobi Theodori Kleinii Naturalem Dispositionem Echinodermatum. 4to, 286 pp. 54 pls. Lipsiae.
49. *Loriol* (afterwards *Loriol-Lefort*), *P. de.* 1880. (Monographie des Échinides contenus dans les couches nummulitiques de l'Égypte.) Mém. Soc. Phys. Genève, vol. xxvii. pp. 59-148, 11 pls.
50. —— 1883. (Eocaene Echinoideen aus Aegypten und der libyschen Wüste.) Palaeontographica, vol. xxx.
51. —— 1884-97. (Notes pour servir à l'étude des Échinodermes, Nos. i.-vi.) Recueil Zool. Suisse, Mém. Soc. Phys. Genève, and Revue Suisse de Zoologie.
52. —— 1887-88. (Faune Crétacique du Portugal. Vol. ii. Échinodermes), 123 pp. 22 pls. Commiss. trav. géol. Portugal.

53. *Loriol-Lefort, P. de.* 1890-91. (Faune jurassique du Portugal, Embranchement des Échinodermes), 179 pp. 29 pls. Commiss. trav. géol. Portugal.

54. —— 1896. (Description des Echinodermes tertiaires du Portugal), 50 pp. 13 pls. Mém. trav. géol. Portugal.

55. *Loriol, P. de, and Desor, E.* 1868-85. Échinologie Helvétique, vol. i. Wiesbaden, 1868-72, 441 pp. 61 pls. ; vol. ii. 1873, in Pictet, Matériaux Paléont. Suisse, sér. 6, No. 2, 398 pp. 33 pls. ; vol. iii. 1875, in Mém. Soc. pal. Suisse, vol. ii. 142 pp. 23 pls. ; 1re Suppl. 1885, 24 pp. 3 pls. *op. cit.* vol. xii.

56. *Lovén, S.* 1867. (Om *Leskia mirabilis*, Gray.) Öfv. Svensk. Vet.-Akad. Förhdl., vol. xxiv. pp. 431-440.

57. —— 1874. (Études sur les Échinoïdées.) Svensk. Vet.-Akad. Handl., vol. xi. No. 7, 91 pp. 53 pls.

58. —— 1883. (On *Pourtalesia*, a genus of Echinoidea.) *Op. cit.* vol. xix. No. 7, 95 pp., 21 pls.

59. —— 1887. (On the Species of Echinoidea described by Linnaeus.) Bihang Svensk. Vet.-Akad. Handl., vol. xiii. Afd. iv. No. 5, 185 pp. 9 pls.

60. —— 1892. (Echinologica.) *Op. cit.* vol. xviii. Afd. iv. No. 1, 74 pp. 12 pls.

61. *Ludwig, H.* 1877. (Ueber bewegliche Schalenplatten bei Echinoideen.) Zeitschr. Wiss. Zool., vol. xxix. pp. 77-86, pl. vii.

62. —— 1890. (Ueber die Function der Madreporenplatte und des Steincanals der Echinodermen.) Zool. Anz., vol. xiii. pp. 377-379.

63. *Mackintosh, H. W.* 1879-83. (The Acanthology of the Desmosticha.) Pt. I. Trans. R. Irish Acad., vol. xxvi. pp. 475-490, pls. ix.-xi. Pt. II. *op. cit.* vol. xxviii. pp. 241-258, pls. v.-viii. Pt. III. *op. cit.* vol. xxviii. pp. 259-266, pls. ix.-x.

64. *Neumayr, M.* 1881. (Morphologische Studien über fossile Echinodermen.) Sitzber. Akad. Wiss. Wien, vol. lxxxiv. pt. i. pp. 143-176, pls. i., ii.

65. —— 1889. Die Stämme des Thierreiches, vol. i. 8vo, vi. and 603 pp. Wien.

66. *Orbigny, A. D. d'.* 1853-55. (Échinodermes.) Paléont. française, Terrains Crétacées, vol. vi. 597 pp. 206 pls.

67. *Perrier, J. O. E.* 1875. (Recherches sur l'appareil circulatoire des Oursins.) Arch. Zool. Expér., vol. iv. pp. 605-643, pls. xxiii., xxiv.

68. —— 1893. Traité de Zoologie, fasc. ii. (Echinoderms on pp. 781-864.) 8vo, Paris.

69. *Pomel, A.* 1883. Classification méthodique et genera des Échinides vivants et fossiles, 132 pp. 1 pl. Thèse doctorale, Paris. Also in Paléont. de l'Algérie, Zoophytes, fasc. 2.

70. *Prouho, H.* 1888. (Recherches sur le *Dorocidaris papillata.*) Arch. Zool. Expér., ser. 2, vol. v. pp. 213-380, pls. xiv.-xxvi.

71. —— 1890. (Du rôle des Pédicellaires Gemmiformes chez les Oursins.) Compt. Rend. Acad. Sci. Paris, vol. cxi. p. 62.

72. *Sarasin, P. B. and C. F.* 1887. (Die Augen und das Integument der Diadematiden.) Ergeb. Naturw. Forsch. Ceylon, vol. i. Heft 1, pp. 1-18, pls. i.-iii.

73. —— 1888. (Ueber die Anatomie der Echinothuriden und die Phylogenie der Echinodermen.) *Tom. cit.* Heft 3, pp. 83-154, pls. x.-xvii.

74. *Schlüter, Cl.* 1883-92. (Die regulären Echiniden der norddeutschen

Kreide.) Abh. preuss. geol. Landesanst., vol. iv. Heft 1; and new ser. vol. v.; in all 315 pp. 21 pls.

75. *Schlüter, Cl.* 1897. (Ueber einige von Goldfuss beschriebene Spatangiden.) Zeitschr. deutsch. geol. Ges., vol. xlviii. pp. 963-975.

76. —— 1897. (Ueber einige exocyclische Echiniden der baltischen Kreide und deren Bett.) Zeitschr. deutsch. geol. Ges., vol. xlix. pp. 18-50, pls. i., ii.

77. *Stewart, C.* (On Certain Organs of the Cidaridae.) Trans. Linn. Soc. Lond., ser. 2, Zool., vol. i. 1879, pp. 569-572.

78. *Theel, H.* 1892. (On the Development of *Echinocyamus pusillus.*) Nova Acta R. Soc. Sci. Upsala, ser. 3, vol. xv. fasc. 1, No. 6.

79. *Thomson, C. Wyville.* 1861. (On a New Palaeozoic Group of Echinodermata.) Edin. New Phil. Journ., n.s., vol. xiii. pp. 106-117, pls. iii., iv.

80. —— 1874. (On the Echinoidea of the *Porcupine* Deep-Sea Dredging Expeditions.) Phil. Trans., vol. clxiv. pp. 719-756.

81. —— 1876. (Notice of some Peculiarities in the Mode of Propagation of certain Echinoderms of the Southern Sea.) Journ. Linn. Soc. Zool., vol. xiii. pp. 55-79.

82. *Uexküll, J. von.* 1896. (Ueber die Function der Polischen Blasen am Kauapparat der regulären Seeigel.) Mitth. Zool. Stat. Naples, vol. xii. pp. 463-476, pl. xxi.

83. *Wright, T.* 1857-78. Monograph of the British Fossil Echinodermata of the Oolitic Formations, vol. i. Echinoidea, xiv. and 481 pp. 43 pls. London: Palaeontogr. Soc.

84. —— 1864-82. Monograph of the British Fossil Echinodermata of the Cretaceous Formations, vol. i. Echinoidea, xxviii. and 371 pp. 80 pls. London: Palaeontogr. Soc.

85. *Zittel, K. A.* Handbuch der Paläontologie, vol. i. pt. iii. 1879.

INDEX

To names of Classes, Orders, Sub-Orders, and Genera ; to technical terms ; and to names of Authors discussed in the text.

Abacocrinus, 165
abactinal skeletal elements, 109
Abatus, 322
aboral circular sinus (Oph.), 266
Abracrinus, 166
Abrotocrinus, 180
Acacocrinus, 166
Acantharchaster, 251
Acanthaster, 258
Acanthechinus, 309
Acanthocrinus, 201
Acanthocystis, 46
acanthosphenote, 287
Acanthotrochus, 234
accessory intestine, 27
— plates (Ast.), 246
Acentrotremites, 90, 92
Aceste, 322
Achlyonice, 229
Achradocrinus, 178
Achradocystis, 55
Acrochordocrinus, 192
Acrocidaris, 307
Acrocrinus, 159
Acrosalenia, 306
Acroura, 278
actinal furrows (Ech.), 317
— skeletal elements, 109
Actinocrinus, 169
Actinocucumis, 230
actinogonidial, 237
actino-lateral spines, 256
Actinometra, 196
Actinophyma, 310
Actinopoda, 227
actinostomial ring (Ast.), 241
Actinozoa (Leuckart), 33
adambulacral, 20
— mouth, 247
adambulacrals (Crin.), 115 ; (Ast.), 241 ; (Oph.), 270
Adelocrinus, 201
Adelopneustes, 316
Adetinae, 321
adetopneustic, 254
adradii, 20
Adunata, 155
Aeolopneustes, 313
Aërope, 322
Aesiocrinus, 180
Aesiocystis, 208
Aethocystis, 57
Aetites, 53
Aganaster, 275
Agaricocrinus, 167
Agassiz, A., 240, 285
Agassiz, L., 240, 260, 261, 284
Agassizia, 322
Agassizocrinus, 181
Agelacrinoidea, 205
Agelacrinus, 207
Agelacystis, 207
Ageladiscus, 208
Agriocrinus, 156
Aldrovandus, U., 283
Alecto, 195
Alexandria, 318
Allagecrinus, 151
Allionia, 201
Allocrinus, 162
Allocystis, 72
Alloprosallocrinus, 167
Amblacrinus, 156
Amblypneustes, 313
Amblypygus, 320
ambulacra, 2, 15 ; (Blast.), 78 ; (Ech.), 286
ambulacralia, ambulacrals (Crin.), 100, 115 ; (Ast.), 241 ; (Ech.), 288, 296
ambulacral mouth, 247
amnion (Ech.), 15
amoebocytes, 22
Amorphocystis, 55
Ampheristocrinus, 173
Amphiaster, 254
Amphiglypha, 278
Amphilepis, 278
Amphipholis, 278
amphisternous, 318
Amphiura, 278
Amphora, 169
Amphoracrinus, 170
Amphoracystis, 47
Amphoridea, 43
ampulla, 290
Amygdalocystis, 58
anal plates (Crin.), 119 ; (Ech.), 294
— spiracle, 85
— tube, 131
— x, 119
Ananchytes, 321
Anapta, 234
Anasterias, 258
Anaulocidaris, 314
anchylosis, 108
Ancyrocrinus, 177
anectobranchiate, 304
Anisocrinus, 189
Ankyroderma, 233
Anochanus, 320
Anomalanthus, 318
Anomalocrinus, 146
Anomalocystis, 51
Anorthopygus, 320
Antedon, 195
Anthenea, 253
Anthenoides, 253
Anthocystis, 62
Anthemocrinus, 200
Anthocrinus, 176
antimeres, 19
Aorocrinus, 167
Aphroditaster, 251
apical nervous system, 30
— system (Crin.), 112 ; (Oph.), 268 ; (Ech.), 286, 294. See also calycinal
Apiocrinus, 191
Apiocystis, 61

Aplocrinus, 151
Apneumona, 226
Apodes, 226
Aporita, 69
Aporocrinus, 201
Apostolides, N. C., 261
Arachniopleurus, 312
Arachnocrinus, 175
Arachnocystis, 54
Arachnoides, 318
Arbacia, 308
Arbacina, 307
arcade-like spaces (Ast.), 248
Archaeocidaris, 302
Archaeocrinus, 200
Archaeodiadema, 308
Archaeopneustes, 321
Archaster, 251
Archasterias, 250
Archegocystis, 73
Archiacia, 321
Argaster, 250
Argopatagus, 323
Aristocrinus, 190
Aristocystis, 44
Aristotle, 218, 283
arm (Crin.), 112; (Ast.), 241; (Oph.), 262, 267, 270. See also brachia
— facet, 100
— pores, 130
Arthracantha, 158
Arthraster, 255
article basal, 108
articles brachiaux, 204
Articulata (Bather), 178; (Jaekel), 141; (Miller), 138; (Müller), 138; (W. & Sp.), 139
articulation (Crin.), 108
Articulosa (Jaekel), 141; (W. & Sp.) 140
Ascidiastella, 218
Ascocystis, 77
Aspidocrinus, 201
Aspidodiadema, 308
Aspidosoma, 250
Aspidura, 278
Asteria, 201
Asterias, 201, 258
— *rubens*, 241
Asteriatites, 201
Asterid plane, 21
Asterina, 254
Asternata, 320
Asteroblastus, 80
Asterocrinus (Lyon), 159
— (Münst.), 201
Asterocystis, 80
Asterodiscus, 254
Asterodon, 253
Asteroidea, 239; diagnosed, 248
Asteropsis (Cott.), 309
— (M. & T.), 254
Asterostoma, 321
Asthenosoma, 311
Astrella, 252
Astriclypeus, 317
Astrios, 202
Astroceras, 276
Astrochele, 276
Astrocnida, 276
Astrocoma, 202
Astrocrinus (Austin), 91
— (Conr.), 161
— (Cumb.), 202
Astrocystites, 209
Astrodon, 276
Astrogomphus, 276
Astrogonium, 253
Astronyx, 276
Astropecten, 252
Astrophyton, 276
Astropodia, 202
Astroporpa, 276
Astropyga, 310
Astroschema, 276
Astrotoma, 276
Astylocrinus, 181
Ataxocrinus, 146
Atelecrinus, 195
Atelecystis, 51
Atelestocrinus, 179
Atelostomata, 318
Atocrinus, 202
Aulocrinus, 180
Auricularia, 5, 225
Austinocrinus, 183
Australanthus, 321
axial canal, 101
— cord, 12, 103
— organ, 23; (Ech.), 291
— sinus, 22; (Crin.), 103; (Ast.) 243; (Oph.), 266
axillare, axillary, 114
Ayers, H., 32
azygos plates, 204

Bactrocrinus, 173
Baculocystis, 46
Baerocrinus, 145
Balanocrinus (Ag.), 182
— (Troost), 202
Balanocystis, 77
Barrande, J., 44, 48
Barrandeocrinus, 166
Barycrinus, 179
basalia, basals (Crin.), 99, 122; (Ast.), 246; (Ech.), 294; (Oph.), 268
Bathybiaster, 252
Bathycrinus, 186
Bathyplotes, 227
Batocrinus, 167
Baueria, 306
Baur, A., 218
Baur's vesicles, 32
Bdellacoma, 254
Belemnocrinus, 152
Belemnocystis, 51
Bell, F. J., 261, 285, 326
Belon, P., 218
Benthaster, 257
Benthodytes, 229
Benthopecten, 251
Beyrichocrinus, 168
bifascial articulation, 117
Bipinnaria, 5, 248
biscuit spicules (Hol.), 224
biserial arms, 115
bivium, 11; (Hol.), 220; (Ech.), 296
Blainville, H. D. de, 240, 260
Blairocrinus, 169
Blakiaster, 251
Blastoidea diagnosed, 78
Blastoidocrinus, 80
Bohadsch, J. B., 218
Bohemicocrinus, 201
Boletia, 313
boss (Ech.), 287
Bothriocidaris, 300
Bothriocidaroida, 300
Botriopygus, 320
Botryocrinus, 179
Bourgueticrinus, 194
bourrelet, 319
brace, 289
brachia, 3, 100, 112. See also arm
brachialia, 100, 204
Brachiocrinus, 146
brachiola, brachioles, 3, 41
Brachiolaria, 6, 248
branchiae (Ech.), 293
branchial vesicles, 245
Brandt, J. F., 226, 240
Breynia, 323
Breynius, J. P., 283
Briarocrinus, 162
Brisinga, 259
Brisingaster, 259
Brissopatagus, 323
Brissopsis, 322
Brissus, 323
Bronn, H. G., 40
buccal fissures, 263
— papillae, 264
— shield, 264
Buch, L. v., 40

Bundenbachia, 274
Bursacrinus, 180
bursae, 26
bursal slit, 264
Bury, H., 218, 240, 261, 285

Cacabocrinus, 164
Cactocrinus, 170
caeca (Ast.), 243
Cainocrinus, 182
Calamocrinus, 192
Calathocrinus (Hall), 170
— (Meyer), 182
Calceocrinus, 148
Calcidocrinus, 201
Calix, 46
Callawaycrinus, 190
Calliaster (Gray), 253
— (Trautsch), 259
Callicrinus, 164
Calliderma, 253
Callocystis, 62
Calocrinus, 202
Calpiocrinus, 189
Calvasterias, 258
Calycanthocrinus, 150
Calycaster, 255
Calycina, 306
calycinal system, 14; (Oph.), 268. See also apical
Calymne, 321
Calyptaster, 257
calyx, 99
Camarocrinus, 77, 161
Camerata (W. & Sp.), 139
— Dicyclica, 198
— Monocyclica, 159
Campanulites, 202
Camptocrinus, 159
canal furrow (Oph.), 262
Canistrocrinus, 161
Capheira, 229
Carabocrinus, 172
Caratomus, 320
Cardiaster, 321
Cardiocystis, 77
Carduocrinus, 179
Carolicrinus, 165
Carpenter, P. H., 14, 44, 91, 139, 140, 182, 325
Carpocrinus, 166
Carpocystis, 73
Caryocrinus, 67
Caryocystis, 55
Caryophyllites, 197
Cassianocrinus, 182
Cassidulus, 321
Castanocrinus, 161
Castocrinus, 148
Catillocrinus, 150
Catopygus, 321
Caudina, 233
Caulaster, 251
Cenocrinus, 182
central blood-plexus, 23
central plate (Oph.), 268
centrale, 135
Centriocrinus, 162
Centrocrinus (Austin), 157
— (W. & Sp.), 162
— (Worthen), 202
centro-dorsal, 135
Centrostephanus, 309
Ceramocrinus, 177
Ceriocrinus (Desor), 191
— (White), 180
Chaetaster, 255
Cheiraster, 251
Cheirocrinus (Eichw.), 63
— (Hall), 148
— (Salter), 148
Cheiroptaster, 257
Chelocrinus, 182
Chiaje, S. Delle, 240, 284, 285
chiasma (Crin.), 114
Chiridota, 234
Chitonaster, 253
Chladocrinus, 182
Cholaster, 275
Chondrocidaris, 302
Choriaster, 254
chromatogen organ, 23
Cidaris, 302
Cidaroida, 301
Cidaropsis, 307
Cigara, 48
ciliated urns, 235
Cionobrissus, 323
Circopeltis, 307
circumoesophageal canal (Ast.), 243; (Oph.), 265. See also Hydrocircus
— nerve-ring (Crin.), 102; (Ast.), 245
cirri, 107, 133
Cirrigrada, 260
Citrocystis, 53
Cladocrinus (Aust.), 189
Cladoidea (Jaekel), 141
Cladophiurae, 276
Claviaster, 321
clavulae, 31
Cleiocrinus, 191
Cleistechinus, 323
Clematocrinus, 156
Clidochirus, 188
cloaca (Hol.), 221
Clonocrinus (Oehl.), 161
Clonocrinus (Quenst.), 162
close suture, 108
Closterocrinus, 173
Clypeanthus, 321
Clypeaster, 318
Clypeastrina, 316
Clypeopygus, 321
Clypeus, 321
Cnemidiaster, 255
Coadunata, 138
Coccocrinus, 156
Codaster, 82, 92
Codechinus, 310
Codiacrinus, 177
Codiacystis, 73
Codiopsis, 309
Codonites, 84
Codonoblastida, 91
Codonocrinus, 202
Coelaster (Sandb.), 259
Coelasterias, 255
coeliac canal, 101
Coeliocrinus, 180
Coelocrinus (M. & W.), 167
— (Salter), 200
coelom, 7
Coelopleurus, 308
collateral organ, 23
Collyrites, 321
Colobocentrotus, 313
Colochirus, 230
Colpaster, 259
columna, 48, 99. See also stem
columnals, 105, 132
Comarocystis, 55
Comaster, 196
Comatula, 195, 196
Comatulina, 202
Comaturella, 202
compass (Ech.), 289
Compsaster, 255
Compsocrinus, 165
Comptonia, 253
Condylocrinus, 201
connective tissue, 28
Conoclypeus, 316
Conocrinus (d'Orb), 194
— (Troost), 202
Conolampas, 321
convoluted organ, 136
Cophinus, 202
Coptodiscus, 316
Coptophyma, 312
Coptosoma, 310
Coraster, 322
Cordylocrinus, 156
corona (Crin.), 99
Coronaster, 258
Coronocrinus, 164

Corylocrinus, 67
Corymbocrinus, 162
Coscinasterias, 258
Cosmasterias, 258
Cosmocrinus, 179
costalia, 141, 204
Costata (Müller), 138 ; (Jaekel), 141
Cottaldia, 309
Cotylecrinus, 198
Cotylederma, 198
Cotyledonocrinus, 159
covering-plates, 101. See also ambulacrals
Craspidaster, 252
Craterina (Barr.), 46
Craterolampas, 321
Cremacrinus, 148
Crenaster (Perr.), 251
Cribrella, 258
Cribrellites (Tate), 259
cribriform organs, 251
Crinocystis, 77
Crinoidea, diagnosed, 94 ; (Jaekel), 141 ; (Müller), 138 ; (Roemer), 33
— brachiata, 94, 138
Cromyocrinus, 181
Crossaster, 256
Crotalocrinus, 176
crown, 99
Crumenaecrinus, 202
Cryptaster, 257
Cryptoblastus, 89, 92
Cryptocrinus, 69
Cryptodiscus, 164
Cryptoschisma, 84, 92
Cryptozonia, 254
Crystallocystis, 53
Ctenaster, 256
Ctenocrinus, 161
Ctenodiscus, 251
Cucumaria, 230
Cuénot, L., 33, 218, 240, 261, 294
Culcita, 254
Culicocrinus, 156
Cupellaecrinus, 156
Cupressocrinus, 177
Cupulaster, 259
Cupulocrinus, 202
Cuvier, G., 1, 218, 226
Cuvierian organs, 223
Cyathidium, 198
Cyathocrinacea, 171
Cyathocrinidae (W. & Sp.), 171
Cyathocrinoidea, 172
Cyathocrinus, 173
Cyathocystis, 208
Cycethra, 254
Cyclaster, 323
Cyclocrinus (d'Orb.), 192
— (Eichw.), 77
Cyclocystoides, 210
Cylicocrinus (S. A. Mill.), 166
Cylicocrinus (Müller), 156
Cypellocrinus (Shum.), 156
— (Stein.), 177
Cyphocrinus, 199
Cyphosoma, 310
Cypressocrinus, 202
Cyrtidocrinus, 188
Cyrtocrinus, 197
Cystaster, 207
Cystasteroidea, 205
Cystechinus, 321
Cystidea, diagnosed, 39
Cystidea (Barr.), 77
Cystoblastus, 64
Cystocidaroida, 300
Cystocrinus, 202
Cytocrinus, 161

Dactylocrinus (Quenst.), 189
— (Slad.), 180
Dactylocystis, 74
Dadocrinus, 182
Daemonocrinus, 202
Decacnemos, 202
Decadactylocrinus, 202
Decadocrinus, 180
Decameros, 202
Deima, 229
deeper oral nervous system, 30
Delocrinus, 180
Deltacrinus, 148
deltoidea, 100. See also oralia
demi-plates, 288
Democrinus, 194
Dendrocrinacea, 171
Dendrocrinoidea, 178
Dendrocrinus, 179
— *cambriensis*, 146
Dendrocystis, 47
dental papillae (Oph.), 272
Derbès, A., 285
dermal branchiae, 245
Dermasterias, 254
desmactinic, 237
Desmidocrinus, 166
Desor, E., 284
Desorella, 320
Deutocystis, 46
Diabolocrinus, 200
Diadema, 309
Diademina, 308
Diademoida, 306
Diademopsis, 309
Diamenocrinus, 200
dibrachialia, 204
Dichocrinus, 159
dichotomy of arms, 112
dicostalia, 204
Dictyaster, 258
Dictyocrinus, 77
Dictyopleurus, 312
dicyclic, 99, 110
Dicyclica, diagnosed, 171
— Camerata, 198
— Inadunata, 171
Dimerocrinus (Pacht), 190
— (Phill.), 198
Dimorphicrinus, 84, 202
Dinocystis, 209
Diplasterias, 258
Dipleurula, 4
Diplocidaris, 303
Diplopodia, 309
diplopores, 41
Diploporita, 70
Diplotagma, 309
Diplothecanthus, 318
Dipneustes, 322
Dipsacaster, 252
Disasterina, 254
disc. (Ast.), 2 ; (Crin.), 99 ; (Oph.), 262
Discocidaris, 302
Discocystis, 208
Discoidea, 316
distal (Crin.), 109
distichalia, 204
Distincta, 178
Dizygocrinus, 168
Dolatocrinus, 164
Dolichocrinus, 197
Doliolocrinus, 202
Donacicrinus, 202
Dorigona, 253
Dorocidaris, 302
dorsal canal, 101
— cup, 99
— fossa, 116
— organ, 23
— shield, 262
dorso-central, 14, 106
Dorycrinus, 167
Dujardin, F., 40, 260, 284
Duncan, P. M., 284, 299, 306
Duvernoy, G. L., 240
Dysaster, 321
Dytaster, 251

Echinanthus, 318
Echinarachnius, 317
Echinaster, 258

Echinasterella, 257
Echinid plane, 21
Echinina, 311
Echinites (Duncan), 316
Echinobrissus, 320
Echinocardium, 323
Echinochrome, 23
Echinocidaris (Dunc.), 308
Echinocorys, 321
Echinocrepis, 324
Echinocrinus (L. Ag.), 202
Echinocucumis, 230
Echinocyamus, 317
Echinocyphus, 312
Echinocystis (Hall), 70
— (W. Thoms.), 301
Echinoderma, diagnosed, 34
Echinodiadema, 309
Echinodiscus (Ag.), 317
— (Worth. & Mill.), 208
Echinoencrinus, 60
Echinoidea, 282
— diagnosed, 299
Echinolampas, 321
Echinometra, 313
Echinonëus, 320
Echinopedina, 310
Echinopsis, 308
Echinosphaera, 53
Echinostrephus, 313
Echinothrix, 310
Echinothuria, 311
Echinozoa, 33
Echinus, 313
— *esculentus*, 285
Ectenocrinus, 146
Ectobranchiata, 306
ectoderm, 30
Edrioaster, 209
Edrioasteroidea, diagnosed, 205
Edriocrinus, 191
Edriocystis, 209
Edwardsocrinus, 157
Elaeacrinus, 88
Elasipoda, 226
Eleutherocrinus, 87, 92
Eleutherozoa, 33
— diagnosed, 217
Elpidia, 229
Emperocrinus, 202
Enallaster, 321
Enallocrinus, 176
Enallopneustes, 321
Encope, 317
Encrinos, 202
Encrinus, 181
Endobranchiata, 300
endocyclic (Ech.), 294
— gut (Crin.), 136
endothecal food-grooves, 41
Enichaster, 321
Enneacystis, 67
Enoploura, 51
Entomaster, 321
Entrochus, 202
Enypniastes, 229
Eocystis, 48
Eodiadema, 308
Eolampas, 321
Eoluidia, 275
Eospondylus, 275
Epactocrinus, 177
Epiaster, 321
epineural canal, 15, 30; (Oph.), 266
epipodium, 288
epithecal food-grooves, 41
epizygal, 108, 117
Eretmocrinus, 167
Erinocystis, 60
Erisocrinus, 181
Etheridge, R. fil., 91, 139
ethmolysian, 295
ethmophract, 295
Euasteroidea, 249
Eublastoidea, 81
Eucalyptocrinus, 164
Euchirocrinus, 148
Eucladia, 275
Eucladocrinus, 158
Eucrinoidea, 139
Eucrinus, 199
Eucystis, 72
Eudesicrinus, 198
Eudiocrinus, 195
Euechinoidea, 299
Eugaster, 274
Eugeniacrinus, 197
Eupachycrinus, 181
Eupatagus, 323
Euphronides, 227
Eupyrgus, 233
Eurhodia, 321
Euryale (König.), 154
— (Lam.), 276
Euryalecrinus, 189
Euryocrinus, 190
Eurypneustes, 313
Euspirocrinus, 173
Eutrochocrinus, 167
Evechinus, 313
exocyclic (Ech.), 294
— gut (Crin.), 136
exothecal processes, 41
external gills, 26
Extracrinus, 182
eye, 32, 245

Fabricius, O., 218
Faorina, 322
fasciole, 319
Faujasia, 321
Ferdina, 255
Fibularia, 317
fimbriated channels (Oph.), 251
finials, 115
Fistulata (Jaekel), 141; (W. & Sp.) 139
Fistulides, 218
fixed brachials, 112
Flabellocrinus, 182
Flexaster, 257
Flexibilia, 140, 187
floscelle, 319
Forbes, E., 260
Forbesiocrinus (Ang.), 189
— (de Kon.), 189
— *Agassizi*, 190
forcipiform pedicellariae, 247
forficiform pedicellariae, 247
food-groove, 100
Freyella, 259
Fromia, 255
Fungocystis, 74
Furcaster, 275

Gagaria, 310
Galeaster, 321
Galerites, 316
Galeroclypeus, 320
Galeropygus, 316
Gammarocrinus, 197
Ganeria, 254
Ganymeda, 203
Gasterocoma, 177
Gastraster, 258
Gastrocrinus, 179
Gaudry, A., 240
Gaurocrinus, 203
Gauthieria, 310
Gazacrinus, 188
Genicopatagus, 321
genital nerve ring, 266
— organs, 24
— plate, 264
— rachis, 101
— ring (Ech.), 291
— scale, 264
— stolon, 23
genitals (Ech.), 286, 294
Gennaeocrinus, 169
Geocoma (Fraas), 195
— (d'Orb.), 278
Geocrinus, 168
Gibbaster, 323
Gilbertsocrinus, 201
Gissocrinus, 175
glandular organ, 23
— pedicellariae, 31

Glaphyrocystis, 60
Glenotremites, 203
Glyphocyphus, 312
Glyptaster, 198
Glyptechinus, 313
Glypticus, 307
Glyptocrinus, 161
Glyptocystidae, 58
Glyptocystis, 64
Glyptosphaera, 73
Gnathaster, 253
Gnathocrinus, 203
Gnathostomata, 315
gnathostomate, 304
Gnorimocrinus, 189
Goldfussia (Norman), 203
Gomphocystis, 77
gonads, 25
Goniaster, 253
Goniasteroidocrinus, 201
Goniocidaris, 302
Goniocrinus, 179
Goniodiscus, 253
Goniodon, 253
Goniopecten, 251
Goniophorus, 306
Goniopneustes, 313
Goniopygus, 307
Gonocrinus, 60
Gorgonocephalus, 276
Gothocrinus, 179
Grammechinus, 313
Grammocrinus, 203
Granatoblastida, 92
Granatocrinus, 90
Graphiocrinus, 180
Grasia, 321
Gray, J. E., 240, 260
Gregory, J. W., 261, 310
Grube, A. E., 226
Gualtieri, N., 284
Gualtieria, 323
Guettardicrinus, 192
Guettaria, 321
gut, 136
Gyllenhal, J. A., 53
Gymnasteria, 254
Gymnobrisinga, 259
Gymnocrinus, 197
Gymnodiadema, 308

Habrocrinus, 166
Hadrocrinus, 164
Haeckel, E., 40, 43, 48, 49, 52, 326
haemal strands, 23
Hagenovia, 321
Haimea, 320
Hallicystis, 61
Halocrinus, 177
Halophenix, 203
Halysiocrinus, 148
Hamann, O., 218, 240, 261
Hapalocrinus, 156
Haplocrinus, 151
Haplocystis, 208
Haplodactyla, 233
haplopores, 41
Harmocrinus, 162
heart, 23
Helianthaster, 258
Heliaster, 258
Helikodiadema, 309
Heliocrinus, 55
Heliocystis, 55
Helmintholithus, 203
Hemiaster, 322
Hemicidaris, 307
Hemicosmites, 66
Hemicrinus, 197
Hemicystis, 207
Hemieuryale, 276
Hemiglypha, 278
Hemipatagus, 321
Hemipedina, 309
Hemipholis, 278
Hemipneustes, 321
Henricia, 258
Hérouard, E., 218
Herpetocrinus, 146
Hertha, 203
Heteroblastus, 90, 92
Heterocentrotus, 313
Heterocidaris, 309
Heteroclypeus, 321
Heterocrinus, 146
Heterocystis, 67
Heterodiadema, 309
Heterolampas, 321
Heterosalenia, 306
heterotomy, 112
Hexacrinus, 158
Hexactis, 240
Hexalacystis, 66
Hibernula, 195
Hippasterias, 253
Hipponoë, 313
Hoffmann, C. K., 285
Holaster, 321
Holectypina, 315
Holectypus, 316
Holocrinus, 182
Holocystis, 47
"*Holocystites*," 72
Holopneustes, 313
Holopus, 197
Holothuria, 227
— *forskali*, 220
Holothurian plane, 20
Holothurioidea, diagnosed, 218
Homalocrinus, 189
Homocrinus, 179
Homocystis, 64
Homoeaster, 323
Homolampas, 323
Hoplaster, 253
Hoplocrinus, 145
Hupé, H., 40, 284
Huxley, T. H., 33
Hybechinus, 313
Hyboclypeus, 320
Hybocrinus, 145
Hybocystis, 95, 145
Hydrasterias, 258
Hydreionocrinus, 180
Hydriocrinus, 180
hydrocircus, 12, 102
hydrocoel, 7
hydrophores palmées, 44, 46, 73
hydropore, 8, 103
hydrospire plates, 86
hydrospires, 83
Hymenaster, 257
Hymenodiscus, 259
Hyocrinus, 153
Hypanthocrinus, 164
Hyperocrinus, 168
Hyphalaster, 251
Hypocrinus, 178
Hyponome, 77, 195
hypostereom, 45
Hypostoma, 260
hypothecal, 2
hypozygal, 108, 117
Hypsospatagus, 323
Hyptiocrinus, 199
Hystricrinus, 158

Ichthyocrinus, 188
Iconaster, 253
Icosidactylocrinus, 203
Idiocrinus, 188
Ilariona, 320
Ilycrinus, 186
Ilyodaemon, 229
imperforate articulation, 108
Impinnata, 187 ; (of P. H. C.), 140
Inadunata dicyclica, 171
— monocyclica, 144
— (W. & Sp.), 139
Inarticulata, 138
Indianocrinus, 145
inferradial, 112
infrabasalia, infrabasals (Crin.), 99, 122 ; (Ast.), 246 ; (Oph.), 268
Infraclypeus, 320
infra-marginals, 246
Infulaster, 321

interambulacra (Ech.), 286
interambulacrals (Crin.), 109, 124; (Ast.), 241; (Ech.), 296
interarticular substance, 28
interaxillaries, 109, 204
interbrachial areas, 246
interbrachials, 109, 118, 204
intercellular substance, 28
intermarginals, 246
internodals, 107
interpinnulars, 118
interradii, 20
intersecundibrachs, 118
Iocrinus, 145
Iraniaster, 323
Irpa, 229
Irregulares (Blastoidea), 91
Irregularia (Crin.), 139; (Ech.), 315
Isaster (Verr.), 251
— (Desor.), 321
Isis, 182
Isocrinus (Meyer), 182
— (Phill.), 189
Isopneustes, 323
isotomy, 112

Jackson, R. T., 299, 302
Jaeger, G. F., 226
Jaekel, O., 114, 116, 141, 154, 171, 300
jaw (Oph.), 263
— plate, 264
Jeronia, 321
Juglandocrinus, 67

Kallispongia, 203
kidney, 23
klasma-plates, 297
Klein, J. T., 283
Kolga, 229
Koninckocidaris, 302
Koninckocrinus, 203
Korethraster, 256
Kowalevsky, A., 218
Krohn, A., 240, 261, 284

Labidiaster, 259
Labidodemas, 227
lacunar plexus, 102
— system, 26
Laetmogone, 229
Laganum, 317
Lageniocrinus, 152
Lahuseniocrinus, 200
Lamarck, J. P. B., 226, 240, 260, 284
Lambertiaster, 323
Lampadaster, 321
Lampterocrinus, 199
lancet-plate, 82
Lanieria, 316
Lankester, E. Ray, 33
Lapillocystis, 46
Lapworthura, 275
Larvata, 141
Larviformia, 139
Lasiaster, 254
lateral arm-plates, 270
Laubeocrinus, 170
Lebrunaster, 254
Lecanocrinus, 188
Lecythiocrinus, 177
Lecythocrinus, 175
Leiaster, 255
Leiocyphus, 312
Leiopedina, 313
Leiosoma, 310
Lenita, 317
Lepadocrinus, 61
Lepadocystis, 61
Lepidaster, 255
Lepidesthes, 305
Lepidocentrus, 301
Lepidocidaris, 302
Lepidodiscus, 208
Lepidopleurus, 312
Lepocrinites, 61
Leptaster, 253
Leptasterias, 258
Leptocidaris, 307
Leptocrinus, 166
Leptocystis, 204
Leptogonaster, 253
Leptoptychaster, 252
leptostroterate, 254
Leske, N. G., 284
Leskia, 323
Leuckart, R., 2, 33, 326
Leucophthalmus, 53
Lichenocrinus, 133
Lichenocystis, 56
Lichenoides, 56
ligament tissue, 28
ligamentar fossae, 116
Linchophorus, 323
Linck, J. H., 239, 260
Linckia, 255
Linnaeus, C., 53, 240, 260, 284
Linopneustes, 323
Linthia, 323
Lithocrinus, 189
Ljungman, A., 260
Lobocrinus, 168
Lobolithus, 77, 136, 161
Lodanella, 46
Lonchotaster, 251
loose suture, 108
Lophaster, 256
Lophocrinus, 179
Loriolaster, 257
Lovén, S., 14, 32, 285
Lovén's plane, 21
Lovenia, 323
Ludwig, H., 218, 226, 240, 261
Luidia, 252
Luidiaster, 251
lunules, 293
Lyman, T., 261
lymph gills, 245
— gland, 23, 27
Lyriocrinus, 200
lysactinic, 237
Lysechinus, 305
Lysocystis, 70
Lysophiurae, 274
Lytaster, 258

M plane, 20
Macarocrinus, 166
MacBride, E. W., 13, 14, 240, 261, 285, 325
Mackintosh, H. W., 285
Macraster, 321
Macrocrinus, 168
Macrocystella, 56
Macropneustes, 323
Macrostylocrinus, 162
madreporic gland, 23
madreporite, 11; (Ast.), 241; (Ech.), 286. See also hydropore
Magnosia, 309
main-axil, 114
Malocystis, 58
mamelon, 287
Mammaster, 255
Maretia, 323
marginals, 241, 246
Marginaster, 254
Mariacrinus, 161
Marsipaster, 257
Marsipocrinus, 156
Marsupiocrinus (Blainv.), 185
— (Hall), 200
— (Phill.), 156
Marsupites, 185
marsupium, 256
Mastigocrinus, 179
Mayraster, 257
Meckel, J. F., 240
Mediaster, 253
Medusacrinus, 203
Medusaster, 259
Meekocystis, 61
Megacystis, 47
Megalaster, 321
Megistocrinus, 168
Melitella, 317

Mellita, 317
Melocrinoidea, 160
Melocrinus, 161
Melonites, 304
Melonitoida, 303
Meoma, 323
meridosternous, 318
Merocrinus, 178
Meseres, 227
Mesoblastus, 90, 92
Mesocrinus, 194
Mesocystis, 75
mesostereom, 45
Mesothuria, 227
Mespilia, 313
Mespilocrinus (de Kon.), 188
— (Quenst.), 192
Mespilocystis, 77
Metablastus, 87, 92
Metacrinus, 183
Metalia, 323
Metaporhinus, 321
Metopaster, 253
Metrodira, 255
Metschnikoff, E., 218, 285
Micraster, 323
Microcrinus, 203
Microcyphus, 313
Microdiadema, 309
Microlampas, 321
Micropedina, 310
Micropocrinus, 198
Micropsina, 313
Micropsis, 310
Micropyga, 309
miliary granules, 287
Miller, J. S., 97, 138
Miller, S. A., 47, 260
Millericrinus, 191
Milletia, 321
Mimaster, 253
Mimocystis, 56
Miospondylus, 275
Missouricrinus, 153
Mitelephaster, 253
Mithrodia, 258
Mitraster, 253
Mitrocrinus, 203
Mitrocystis, 50
Moira, 323
Moiropsis, 323
Molpadia, 233
Monaster, 250
monocyclic, 99, 110
Monocyclica, diagnosed, 144
— Camerata, 159
— Inadunata, 144
Monophora, 317
Monostychia, 318
Moriaster, 252
Mortonia, 317
Moulinsia, 317
mouth-frame, 263
mouth papillae, 241
Muelleria, 227
Müller, Joh., 40, 138, 218, 240, 260, 261, 285
muscle fibres, 27
muscle fields, 262
— fossae, 116
Mycocrinus, 150
Myelodactylus, 146
Myriotrochus, 234
Myrtillocrinus, 177
Myxaster, 257

Nacospatangus, 323
Nanocrinus, 177
Narcissia, 255
Nardo, J. D., 240
Nardoa, 255
Nectria, 253
Nematocrinus, 150
Neocatopygus, 321
Neocrinoidea, 139
Neocrinus, 182
Neocystis, 77
Neolampas, 321
Neomorphaster, 255
Neoplax, 276
Neopneustes, 323
Nepanthia, 254
Neumayr, M., 44, 48, 49, 326
Neviani, A., 310
Nidorellia, 254
Nipterocrinus, 188
nodals, 107
Nucleocrinus, 88, 92
Nucleolites, 320
Nucleopygus, 320
Nymphaster, 253

oculars, 286, 294
Odinia, 259
Odontaster, 253
odontophore (Ast.), 247
Offaster, 321
Ogmaster, 253
Ohiocrinus, 146
Oken, L., 226
Oligopodia, 320
Oligoporus, 304
Oligopygus, 320
Olivanites, 88
Ollacrinus, 201
Oncocrinus, 187
Oneirophanta, 229
Onychaster, 275
Onychocrinus, 190
Oolaster, 321
Opechinus, 312
Ophiacantha, 278
Ophiactis, 278
Ophiarachna, 277
Ophiarthrum, 278
Ophidiaster, 255
Ophiernus, 278
Ophioblenna, 278
Ophiobyrsa, 276
Ophiocamax, 278
Ophiocentrus, 278
Ophioceramis, 278
Ophiochiton, 278
Ophiochondrus, 276
Ophiochytra, 278
Ophiocnemis, 278
Ophiocnida, 278
Ophiocoeta, 277
Ophiocoma, 278
Ophioconis, 277
Ophiocreas, 276
Ophiocrene, 276
Ophiocrinus (Ang.), 179
— (Charlesw.), 146
— (Salter), 201
— (Semper), 195
Ophiocten, 278
Ophiocymbium, 278
Ophioderma, 277
Ophiogeron, 276
Ophioglypha, 278
Ophiogona, 277
Ophiogymna, 278
Ophiohelus, 276
Ophiolebes, 278
Ophiolepis (Lyman), 278
— (M. & T.), 278
Ophiomartus, 278
Ophiomastix, 278
Ophiomaza, 278
Ophiomitra, 278
Ophiomusium, 278
Ophiomyces, 276
Ophiomyxa, 276
Ophionema, 278
Ophionephthys, 278
Ophionereis, 278
Ophiopaepale, 278
Ophiopege, 275
Ophiopeltis, 278
Ophiopeza, 277
Ophiopholis, 278
Ophiophragonus, 278
Ophiophyllum, 278
Ophioplax, 277
Ophioplinthus, 278
Ophioplocus, 278
Ophiopsamnium, 278
Ophiopsila, 278
Ophiopteris, 278

Ophiopteron, 278
Ophiopus, 278
Ophiopyren, 277
Ophiopyrgus, 277
Ophiosciasma, 276
Ophiostigma, 278
Ophioteresis, 276
Ophiothamnus, 278
Ophiothela, 278
Ophiotholia, 276
Ophiothrix, 278
Ophiotrema, 278
Ophiotrochus, 278
Ophiozona, 278
Ophiura, 278
— *ciliaris*, 262
Ophiurella, 278
Ophiurina, 275
Ophiuroidea, 259
— diagnosed, 273
oral angle (Ast.), 246
— — plates (Oph.), 263
— nerve-ring, 102
— nervous system, 30
— papillae, 264
— ridge (Blast.), 82
— skeleton (Ast.), 241
orals, 124. See also deltoids
Orbitremites, 90, 92
Orcula, 230
Oreaster, 254
orientation of crinoid, 110
Oriolampas, 321
Ornithaster, 323
oro-central, 14
Orocystis, 54
Orophocrinus, 84, 92
Orthechinus, 310
Orthocidaris, 302
Orthocrinus, 198
Ortholophus, 312
Orthopsis, 308
oscular orifice, 256
otocysts, 32
Ottawacrinus, 178
outer side-plates (Blast.), 84
Oviclypeus, 316
ovoid gland, 23. See also axial organ
Ovulaster, 321

Pachyantedon, 203
Pachyclypeus, 316
Pachycrinus, 203
Pachylocrinus, 180
Pachyocrinus, 203
Paelopatides, 227
Palaeaster, 250
Palaeasterina, 250
Palaeasteroidea, 249
Palaeëchinasteridae, 250
Palaeëchinoidea, 299
Palaeëchinus, 304
Palaeobrissus, 322
Palaeocoma, 254
Palaeocrinoidea, 139
Palaeocrinus, 172
Palaeocystis, 54
Palaeodiscus, 301
Palaeolampas, 321
Palaeonectria, 250
Palaeophiura, 274
Palaeopneustes, 322
Palaeostella, 250
Palaeostoma, 323
Palaeotropus, 323
Palasteriscus, 257
Palastropecten, 275
Pallas, P. S., 218
Palmacystis, 73
palmaria, 204
Palmipes, 254
palps (Ast.), 245
Pannychia, 229
papulae, 26, 245, 248
parabasalia, 99
Paractinopoda, 234
Paradoxechinus, 312
Paragonaster, 253
Paralampas, 321
pararadials, 150
Pararchaster, 251
Parasalenia, 313
Parelpidia, 229
parietal canal, 9
Parisocrinus, 173
Pasceolus, 77
Patelliocrinus, 162
patina, 112
Patiria, 254
Paulia, 254
paxillae, 247
Pectinaster, 251
pectinirhombs, 43, 58
Pectinura, 278
Pedatae, 226
pedicellariae, 31; (Ast.), 247; (Ech.), 287
Pedicellaster, 258
Pedina, 309
Pedinopsis, 313
Pedinothuria, 310
Pelagothuria, 230
Pelanechinus, 310
pellions, 289
Pelmatozoa, 33
— diagnosed, 38
Pelmatozoic ancestor, 9
Peltastes, 306
Pendulocrinus, 148
Peniagone, 229
Pentaceropsis, 254
Pentaceros, 254
Pentacrinus, 182
Pentactæa, 12
Pentactula, 18
Pentadia, 181
Pentagonaster, 253
Pentagonites, 203
pentameres, 99
Pentephyllum, 90, 93
Pentremites, 86, 92
Pentremitidea, 85, 92
perforate articulation, 109, 116
Peribolaster, 256
Pericosmus, 323
Periechocrinus, 168
Periglyptocrinus, 161
perignathic girdle, 289, 297
peri-intestinal cavity, 103
perioesophageal sinus, 22
periproct, 286
Perischodomus, 302
— *magnus*, 203
perisoma, 241
peristome (Crin.), 97; (Ech.), 285
peristomial plates (Oph.), 264
Perknaster, 258
Peronia, 308
perradii, 19
Perrier, E., 241, 259, 285
Persephonaster, 251
Petalocrinus, 175
Petinocrinus, 203
Petraster, 250
Phaenoschisma, 84, 92
Phaneraster, 253
Phanerozonia, 249
Phanogenia, 196
Pharia, 255
pharyngeal vesicles, 27
Phialocrinus (Eichw.), 203
— (Trautsch.), 181
Phillipsocrinus, 170
Philocrinus, 180
Phimocrinus, 152
Phoenicocrinus, 166
Pholidaster, 255
Pholidocidaris, 305
Phormosoma, 311
Phoxaster, 252
Phyllobrissus, 321
Phylloclypeus, 321
Phyllocrinus, 197
phyllode, 319
Phyllophorus, 230
Phymechinus, 309
Physetocrinus, 170

Phytocrinus, 195
Pictet, F. J., 40
Picteticrinus, 182
Pileus, 316, 320
Pilocystis, 46
Pinnata (P. H. Carp.), 140 ; (Bather), 191
pinnulae, 113
Pionocrinus, 166
Pirocystis, 47
Pisocrinus, 149
Placocystis, 51
Placodiadema, 309
plastidogen organ, 23
Platasterias, 252
Platybrissus, 322
Platyceras, 157
Platycrinus, 157
Platycystis, 51
Platysphaerites, 203
Plectaster, 258
Plesianthus, 318
Plesiocidaroida, 305
Plesiolampas, 321
Pleurechinus, 312
Pleurocrinus, 157
Pleurocystis, 64
Pleurodiadema, 309
plexiform gland, 23
Plicatocrinus, 153
Pliny, 218
Plistophyma, 309
Plumaster, 259
Pluteus, 6, 16 ; (Oph.), 273
Plutonaster, 251
Pneumophora, 226
Podasterias, 258
podia, 1, 2 ; (Ast.), 243 ; (Ech.), 291
Podocidaris, 308
Polian vesicles, 27 ; (Ast.), 243 ; (Ech.), 291
Polyasterias, 258
Polycerus, 182
Polycidaris, 302
polycyclic spine, 287
Polycyphus, 310
Polypeltes, 162
Polypholis, 278
Pomatocrinus, 191
Pomel, A., 284
Pomocystis, 72
Pomonites, 72
Pomosphaera, 72
Pontaster, 251
Porania, 254
Poraniomorpha, 254
Porcellanaster, 251
pore canal, 8
— plate, 80
— rhombs, 42
pores, ambulacral (Ech.), 287
— of Blastoids, 86
Porocrinus (Bill.), 172
— (Dittm.), 182
postpalmaria, 204
Poteriocrinacea, 171
Poteriocrinidae (W. & Sp.), 171
Poteriocrinus, 180
Pourtalesia, 323
Pradocrinus, 168
Prenaster, 323
pre-oral lobe, 4, 8
primary skeletal elements, 109
primaxil, 114
primibrachs, 114
primitive suture, 108
Proclivocrinus, 148
Prognaster, 255
Promachocrinus, 195
Protaster, 274
Protasteracanthion, 251
Proteocystis, 73
Proteroblastus, 74
Proteuryale, 203
Protoblastoidea, 79
Protocrinus, 74
Protocyamus, 316
Protocystis, 48
Prouho, H., 245, 285, 288
proximal (Crin.), 109
proximale, 108
Prunocystis, 60
Prymnadetinae, 322
Prymnodesminae, 323
Psammechinus, 313
pseudambulacra (Cyst.), 43 ; (Blast.), 78
Pseudarchaster, 251
Pseudaster, 251
pseudhaemal ring, 102
— system, 25 ; (Ast.), 243 ; (Ech.), 292
Pseudoboletia, 313
Pseudocatopygus, 321
Pseudocrinus, 62
Pseudocucumis, 230
Pseudodesorella, 321
Pseudodiadema, 309
pseudo-heart, 23
pseudomonocyclic, 111
pseudo-pedicellariae, 247
Pseudopedina, 309
Pseudostichopus, 227
Psilaster, 252
Psolidium, 230
Psolus, 230
Psychropotes, 229
Psychrotrephes, 229
Pterocoma, 203
Pterotocrinus, 159
Ptilonaster, 274
Ptychocrinus, 198
Pupa, 5
Pycnaster, 253
Pycnocrinus, 161
Pycnopodia, 258
Pycnosaccus, 187
Pygaster, 316
Pygastrides, 316
Pygaulus, 320
Pygorhynchus, 321
Pygorhytis, 321
Pygospatangus, 323
Pygurostoma, 321
Pygurus, 321
pyramids (Ech.), 289
Pyrina, 320
Pyrocystis. See *Pirocystis*
Pythonaster, 257
Pyxidocrinus, 168

radial canals, 243. See also perradial
— dome-plates, 127
— facet, 100
— pseudhaemal canal, 100
— shields, 264
— sinus, 84
— vesicles, 27
radialia, radials (Crin.), 99, 204 ; (Ast.), 246 ; (Ech.), 294 ; (Oph.), 268
radianal, 112, 119
Radiaster, 254
Radiata, 2
radical cirri, 107
Radiocyphus, 312
radix, 99
rami, 113
ramuli, 113
rectal caeca, 243
recumbent arms, 43, 65
Regulares (Blast.), 91
Regularia (Crin.), 139
— Ectobranchiata, 306
— Endobranchiata, 300
Remaster, 256
respiratory trees, 27, 222
Retaster, 257
rete mirabile, 223
Reteocrinus, 198
Rhabdocidaris, 302
Rhabdopleurus, 312
Rhadinocrinus, 179
Rhaphanocrinus, 200
Rhegaster, 254
Rhinobrissus, 323
Rhipidaster, 256
Rhipidocrinus, 201

Rhizocrinus, 194
Rhodocalix, 203
Rhodocrinus, 201
Rhoëchinus, 304
Rhombifera, 52
Rhombifera (Barr.), 57
— *mira*, 77, 145
Rhopalocoma, 257
Rhopalocrinus, 191
Rhopalodina, 230
Rhynchopygus, 321
Roemeraster, 255
Romanes, G. J., 245
Rondelet, W., 218, 283
root, 99
Rosaster, 253
rosette (Crin.), 195 ; (Ech.), 289
Rotula, 317
Rotuloidea, 317
Rouault, M., 45
Runa, 317
Russo, A., 261

Saccocoma, 154
Saccocrinus, 168
sacculi, 137
Sagenocrinus, 190
sagittal plane, 20
Salmacis, 312
Salmacopsis, 312
Salenia, 306
Salter, J., 260
Salteraster, 251
Sampsonocrinus, 170
Sarasin, P. & F., 32, 285, 310, 326
Sarsella, 323
Scaphiocrinus, 180
scapula, 204
Schizaster, 323
Schizoblastus, 89, 92
schizocoelic system, 26
Schizocrinus, 161
Schizocystis, 61
Schoenaster, 250
Sclerasterias, 258
Sclerocrinus, 197
Scoliocrinus, 178
Scoliocystis, 60
Scolocystis, 70
Scotoanassa, 229
Scotoplanes, 229
scrobicular circle, 287
scrobicule, 287
scuta adoralia, 264
Scutella, 317
scutella oralia, 263
Scutellina, 317
scutum buccale, 264
Scyphocrinus (Hall), 161
Scyphocrinus (Zenker), 161
Scytactinota, 218
Scytalecrinus, 180
Scytodermata, 33, 218
Seba, A., 284
secondary skeletal elements, 109, 204
— radials, 204
secundibrachs, 114
segmental apertures, 256
Selenka, E., 218, 226
Semi-Articulata, 138
Semon, R., 12, 18, 218
Semper, K., 218
sensory buds, 31
sessile pedicellariae, 247
Shumardocrinus, 203
side-plates, 82
Sigsbeia, 276
Simroth, H., 261
Siphonocrinus, 199
Sismondia, 317
Sitularia, 185
Sladen, W. P., 14, 240, 251, 259, 261, 325
Smilasterias, 258
Solacrinus, 203
Solanocrinus, 195
Solaster, 256
Spatagocystis, 324
Spatangomorpha, 323
Spatangus, 323
Sphaeraster, 254
Sphaerechinus, 313
sphaeridia, 32
Sphaerites (Quenst.), 19, 254
Sphaerocrinus (M. & W.), 167
— (Roem.), 173
Sphaerocystis, 63
Sphaeronis, 71
Sphaerothuria, 230
Sphenocrinus, 203
spines (Ech.), 285, 287
Spinigrada, 260
spiracula, spiracles (Blast.), 84 ; (Ast.), 256
spongy organ, 27, 102
Sporasterias, 258
Springer, F. See Wachsmuth
Spyridiocrinus, 163
Statozoa, 33
Staurocystis, 61
Staurosoma, 57
Steganoblastus, 209
Steganocrinus, 170
Stegaster, 321
Stegmaster, 254
Steinmann, G., 40
Stelidiocrinus, 161
Stella, 260
Stellae fissae, 240
Stellaster, 253
Stelleroidea, 237
— diagnosed, 239
stem, 48, 99, 105, 132. See also columna
Stemmatocrinus, 181
Stenaster, 251
Stenocrinus, 146
Stenonia, 321
Stephanaster, 253
Stephanocrinus, 96, 145
Steraster, 257
Stereocidaris, 302
Stereocrinus, 164
stereom, 28
Sternata, 321
Sternotaxis, 321
sternum (Ech.), 318
Stewart, C., 285
Stewart's organs, 303
Stichaster, 255
Stichocystis, 55
Stichopus, 227
Stigmatopygus, 321
Stirechinus, 313
stomach (Ast.), 243
Stomatocrinoidea, 139
Stomechinus, 309
Stomopneustes, 313
Stomoporus, 323
stone-canal, 8 ; (Ast.), 243 ; (Ech.), 291
Stortingocrinus, 152
Streptaster, 208
Streptocrinus, 179
Streptophiurae, 274
streptospondyline, 271
Stribalocystis, 67
Strobilocystis, 63
Stromatocystis, 207
Strongylocentrotus, 313
Strophocrinus, 172
Strotocrinus, 170
Studeria, 321
Stürtz, B., 250, 260
Sturtzura, 274
Stylocrinus, 152
Styracaster, 251
subanale, 204
subepithelial nervous system, 30
sub-lancet, 85
suboralia, 141
subradiale, 204
subradialia, 204
subtegumentary cavity, 103
subtentacular canals, 100
superbasals, 159

super-radial, 112
supplementary plates, 109, 204
supra-marginals, 246
suranal, 294
sutures, 108
Sycocrinus, 203
Sycocystis, 60
Symbathocrinus, 152
Symphytocrinus, 197
Synallactes, 227
Synapta, 234
Synerocrinus, 190
syngnaths, 263
Synyphocrinus, 180
Syringocrinus, 48, 203
syzygy, 108, 117

tables (Hol.), 223
Taeniaster, 251
Taeniura, 274
Talarocrinus, 159
Tanaocrinus, 165
Tarsaster, 255
Taxocrinus, 189
Technocrinus, 163
tegmen, 99, 129
Teleiocrinus, 170
Temnechinus, 312
Temnocidaris, 302
Temnopleurus, 312
tentacles (Hol.), 224
terminal tentacle, 31
terminals (Ech.), 294
tertibrachs, 114
Tesselata (Zittel), 139
Tessellata (Müller), 139
test (Ech.), 285
Testacea, 138
Tetanocrinus, 197
Tethyaster, 251
Tetracidaris, 303
Tetracrinus (Austin), 203
— (Münst.), 153
Tetractis, 240
Tetramerocrinus (Austin), 204
Tetraster, 250
Thalamocrinus, 204
Thallocrinus, 156
Thaumatocrinus, 196
theca, 99
Thecocystis, 207
Thecoidea, 205
Théel, H., 15, 218, 226
Theelia, 230
Thegaster, 317
Thenarocrinus, 179
Thiolliericrinus, 195
Tholaster, 321
Thoracaster, 251
Thylacocrinus, 200
Thylechinus, 310
Thyone, 230
Thyroida, 205
Thysanocrinus, 198
Tiaracrinus, 57
Tiarechinus, 305
Tiedemann, F., 218, 240, 284
Tiedemann's bodies, 27, 243
Tonia, 255
Tormocrinus, 197
Tornaria, 5
torus angularis, 264
Torynocrinus, 197
Toxaster, 322
Toxopneustes, 313
Traumatocrinus, 182
Trautschold, H., 130
Tremaster, 254
Tremataster, 275
Trematocrinus, 201
Trematocystis, 72
Trematopygus, 320
Triacrinus, 149
Trianisites, 204
tribrachialia, 204
Tribrachiocrinus, 181
Trichaster, 276
Trichasteropsis, 250
Trichocrinus, 149
Trichotaster, 259
Tricoelocrinus, 87, 92
trifascial articulation, 117
Trigonocidaris, 312
Trigonocrinus, 197
Trigonocystis, 50
Trinemacystis, 53
Triplacidia, 310
Triplaricrinus, 204
Tripneustes, 313
Trisactis, 240
trivium, 11; (Hol.), 220; (Ech.), 296
Trochita, 204
Trochocrinus, 168
Trochocystis, 50
Trochoderma, 234
Trochodota, 234
Trochostoma, 233
Troostoblastida, 92
Troostocrinus, 86, 92
Tropidaster, 255
Troschel, F. H., 240, 260
Trybliocrinus, 163
Tuberaster, 323
tubercles (Ech.), 286
Turbinocrinus, 161
Tylaster, 254
Tylocidaris, 302
Typocidaris, 302

Uintacrinus, 183
Ulocrinus, 181
umbo (Ech.), 262
umbonal socket, 263
under lancet-plate, 85
Uniophora, 258
uniserial arms, 115
Uperocrinus, 168
Urasterella, 251
Urechinus, 321

Valentin, G., 284
Valvaster, 258
Vasocrinus, 179
vault, 128
ventral sac, 27
— shield, 262
vertebral ossicle (Oph.), 262
vestibule, 11
Viguier, C., 240, 247
Vletavicrinus, 204
Volborth, A., 53
Vologesia, 321

Wachsmuth, C., 139
Wachsmuth & Springer, 114, 139, 171
Wachsmuth & Springer's Law, 106
Walther, J., 49
water-vascular system (Ast.), 243; (Oph.), 272; (Ech.), 290
Woodocrinus, 180

Xenaster, 250
Xenocrinus (Jahn), 204
— (S. A. Miller), 165

Zeacrinus, 180
Zenkericrinus, 161, 204
Zeuglopleurus, 312
zigzag arms, 115
Zittel, K. A. v., 40, 139, 171
Zophocrinus, 151
Zoroaster, 255
Zygocrinus, 91, 93
Zygophiurae, 277
Zygospondyline, 271

THE UNIVERSITY LIBRARY
UNIVERSITY OF CALIFORNIA, SANTA CRUZ
SCIENCE LIBRARY

This book is due on the last **DATE** stamped below.
To renew by phone, call **429-2050**

MAR 14 1973
REC'D MAR 16
MAY 16 1973
REC'D MAY 4
MAR 28 1980
REC'D MAR 18 1980

30m-9,'72 (Q4585s8)—3A-1

STORED AT NRLF